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THE ESTIMATION OF THE NUMBER OF INDIVIDUALS ENTERING EACH STAGE DURING THE DEVELOPMENT OF ONE GENERATION OF AN INSECT POPULATION

By J. P. DEMPSTER

*Locust Research Team, Cyprus**

(With 2 Figures in the Text)

In their paper on British grasshoppers, Richards & Waloff (1954) describe a method of estimating the mortality in one generation of a population in which the instars overlap, using a series of estimates of the numbers of each instar. Briefly, the theory of this method is as follows. If it is assumed that when once the hoppers have hatched, there is an approximately steady mortality, the time trend of the population will fit the formula $Y = nk^x$, where Y is the population occurring on day x, n is the total number of hoppers which emerge, and k is the fraction surviving each day. The logarithm of Y (for values after the peak) will follow a straight line, since $\log Y = \log n + x \log k$. A linear regression equation can be determined for the logarithm of successive population estimates in conjunction with values of x, and the regression coefficient is the logarithm of the average fraction of the population surviving each day. The size of the initial population can be calculated by means of this equation. A calculation for the population less the first instar (i.e. for successive accumulated totals of the second instar) gives an estimate of the total number of hoppers that have entered the second instar. A corresponding total can be determined for each subsequent instar. From these estimates of the total number of hoppers entering each stage, the mortality during each can be calculated.

The object of this note is to discuss a test of this method of estimating the total number of individuals entering each stage, in a laboratory population of *Locusta migratoria migratorioides* (R. & F.) reared in cages. Twenty-two cages were used, each heated from above by an electric light bulb, and containing sand at the bottom. Green food was placed in each cage twice a day, and the hoppers lived within a temperature and humidity gradient between the sand and the bulb. Thirty-three newly hatched hoppers were placed in each cage, and daily records of deaths and moults made until all were dead. Each batch of hoppers was treated as a unit and their records were combined so as to construct a population with a chosen hatching period of a duration within the range observed in field populations. The order in which batches were used was randomized. The number of batches assigned to each day in the theoretical hatching-curve is shown in Table 1. Most of this work was based on figures obtained from the 17-day hatching period to which Table 1 refers, but figures representing hatching periods of twenty-five and thirty-one days were also used. In this way a population curve showing the

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numbers occurring each day was obtained, and this was used as if it were obtained from field data, to calculate the total number of hoppers for each stage. Each of these estimates was then compared with the corresponding actual number, and the effect of small changes in the method of calculation was observed.

Table 1. *The number of batches of hoppers added to the theoretical population every second day*

	Day								
	1	3	5	7	9	11	13	15	17
Batches	1	1	4	7	4	2	1	1	1

The term 'accumulated total' refers to the number of individuals in a particular instar and any later instars found on any particular day. The need for using accumulated totals instead of figures for a single instar is evident in Table 2. It will be seen that estimates based on single-instar totals are far too high; this is due to the fact that the numbers moulting have been included with the numbers dying. The use of accumulated totals overcomes this difficulty.

Table 2. *Comparison of estimates based on accumulated totals and on totals for single instars with actual counts*

	Instar I	Instar II
Actual counts	726	601
Estimates from accumulated totals	1299	1160
Estimates from single-instar figures	6293	5015

Occasionally the accumulated total of an instar increases to a peak, then decreases for a few days, and finally increases to a second peak. It is then difficult to decide which peak to regard as the starting point of the steady mortality. For this reason a series of estimates was made, treating different parts of the curve as the peak. As would be expected, the best estimates were obtained when using the peak in the accumulated totals nearest to that of the single-instar figures. Estimates obtained by using the actual peak in the single-instar figures, however, are not so good (cf. Table 3).

Table 3. *Comparison of estimates obtained by using the peak of the single-instar figures, and the peak of the accumulated totals, with actual counts*

The figures in brackets in this and subsequent tables are percentage errors.

	I	II	III	IV	V	Average % Error
Actual counts	726	601	546	460	371	—
Estimate from the instar peak	569 (12·8)	516 (14·1)	464 (15·0)	355 (22·8)	291 (21·6)	17·2
Estimate from the peak in the accumulated totals	662 (8·8)	739 (22·9)	559 (2·4)	407 (11·5)	409 (10·2)	11·2

It is possible that mortalities at different stages in the life-cycle are very different. If this is so, one would expect an estimate based on the accumulated totals between the peak and the end of the instar under consideration to be more accurate

than one based on the whole curve beyond the peak. Table 4 shows that this is the case. Estimates based on the single-instar and nymphal portions of the curve are far better than those based on the whole curve. This is chiefly because mortality during adult life is markedly different from that during the nymphal period.

Table 4. *The comparison of estimates based on the whole curve, the nymphal portion of the curve and the single-instar portions of the curve, with actual counts*

	I	II	III	IV	V	Average % Error
Actual counts	726	601	546	460	371	—
Estimate from whole curve	1299 (78·9)	1160 (93·0)	1065 (95·1)	979 (112·8)	874 (135·6)	103·1
Estimate from nymphal portion	633 (12·8)	596 (0·8)	569 (4·2)	544 (18·3)	512 (38·0)	14·8
Estimate from single-instar portions	662 (8·8)	739 (22·9)	559 (2·4)	407 (11·5)	409 (10·2)	11·2

Results obtained with the three hatching periods described earlier are shown in Table 5, together with those obtained when all the hoppers hatch on one day (i.e. when all batches of hoppers are added to the population on day one). It appears that this method gives better results with populations with short hatching periods than with long ones.

Table 5. *Showing the effect of the length of the hatching period on the accuracy of estimates*

	I	II	III	IV	V	Average % Error
Actual counts	726	601	546	460	371	—
Estimate based on a 1-day hatch	740 (1·9)	699 (16·3)	690 (26·4)	437 (5·0)	341 (8·1)	11·5
Estimate based on a 17-day hatch	662 (8·8)	739 (22·9)	559 (2·4)	407 (11·5)	409 (10·2)	11·2
Estimate based on a 25-day hatch	756 (4·1)	698 (16·1)	486 (11·0)	377 (18·0)	451 (21·6)	14·2
Estimate based on a 31-day hatch	510 (29·8)	392 (34·8)	468 (14·3)	355 (22·8)	455 (22·6)	24·9

There is a tendency for a few hoppers to stay in an instar long after the rest have moulted to the next. When this happens, the mortality during a considerable part of the later of the two instars is included with that of the earlier. Estimates were therefore made ignoring these 'tail figures', and this was shown to give a slight average improvement in the results (cf. Table 6).

Table 6. *The effect of ignoring 'tail figures'*

	I	II	III	IV	V	Average % Error
17-DAY HATCH						
Actual counts	726	601	546	460	371	—
Normal treatment	662 (8·8)	739 (22·9)	559 (2·4)	407 (11·5)	409 (10·2)	11·2
'Tail' ignored	570 (12·7)	639 (6·3)	565 (3·5)	393 (14·6)	392 (5·7)	8·6
25-DAY HATCH						
Normal treatment	756 (4·1)	698 (16·1)	486 (11·0)	377 (18·0)	451 (21·6)	14·2
'Tail' ignored	628 (13·5)	637 (6·0)	514 (5·8)	321 (30·2)	426 (14·8)	14·1
31-DAY HATCH						
Normal treatment	510 (29·7)	392 (34·8)	468 (14·3)	355 (22·8)	455 (22·6)	24·9
'Tail' ignored	528 (27·2)	356 (40·7)	460 (15·7)	328 (28·7)	339 (8·6)	24·2

DISCUSSION

A comparison of estimates based on different segments of the population curve (Table 4) indicates that there is a marked difference between mortalities at different stages in the life-cycle. This differential mortality is apparent when the logarithm of Y (for values after the peak) is plotted against x; this gives a sigmoid curve instead of a straight line (Fig. 1). The differences between mortalities at

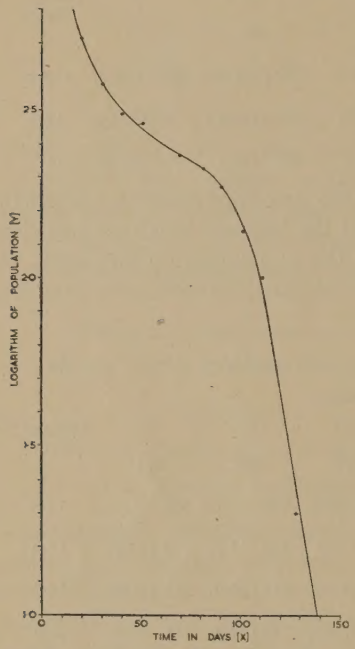

Fig. 1. The sigmoid form of the laboratory population-curve.

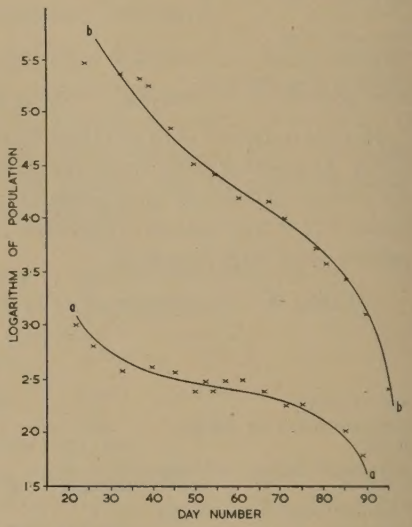

Fig. 2. The shape of the curve obtained by plotting the logarithm of population estimates against time (estimates obtained from *Dociostaurus* populations (*a*) at Kaloyeros and (*b*) at Mia Milea).

different stages in the life-cycle explain why better estimates were obtained from short hatching periods than from long ones. A long hatching period leads to a longer overlapping of the stages, and therefore a greater effect of mortality in the following instars on estimates of population from the one being considered. These data apply to a laboratory population in which there was little mortality during early adult life, and a rapid fall in numbers later when old age took effect. In the field, where there are more numerous causes of death, one would expect a more constant fall in numbers, and the effect of old age to be unimportant. While working in Cyprus, the writer obtained population estimates of *Dociostaurus maroccanus* (Thunberg). A sigmoid curve was obtained when the logarithms of these estimates were plotted against time (Fig. 2), but the curve more nearly approaches a straight line than does that from the laboratory population. The rapid fall in numbers of *Dociostaurus* towards the end of the season is due primarily to the

effects of drought and the destruction of ovipositing females by lizards and other predators.

For many populations, the assumption that mortality is approximately steady after hatching is certainly not true for the whole of the life-cycle. It is, however, likely to be more nearly true over a short period such as the length of a single instar. In general, therefore, it is better to base estimates of the total number entering each stage upon accumulated totals between the peak and the end of the instar that is being considered than on the whole curve. Further, if the duration of an instar is long, better estimates will be obtained by ignoring what are clearly 'tail figures'.

ACKNOWLEDGMENTS

Most of this work was carried out at the Imperial College of Science and Technology, and I am deeply indebted to Professor O. W. Richards and to Dr N. Waloff, for their help and suggestions. I also wish to thank Dr B. P. Uvarov, of the Anti-Locust Research Centre, both for his advice and for the award of a scholarship which enabled this work to be done.

SUMMARY

The methods described by Richards & Waloff (1954) of estimating the mortality in one generation of an insect population, in which the instars overlap, is discussed with reference to a laboratory population of *Locusta migratoria migratorioides* (R. & F.). A general indication is given of the best way of obtaining estimates by this method.

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Richards, O. W. & Waloff, N. (1954). Studies on the Biology and Population Dynamics of British Grasshoppers. *Anti-Locust Bull.* No. 17.

THE RELATIONS BETWEEN THE BED MEDIUM OF SEWAGE FILTERS AND THE FLIES BREEDING IN THEM*

By R. J. TERRY

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(With 3 Figures in the Text)

INTRODUCTION

The fauna of sewage filter beds is dominated by certain species of flies and worms, which play an important part in sewage purification processes as they feed on the bacterial, algal and fungal matter which develops in the bed. This growth, if unchecked, would soon block the filter and make it useless for purification. Experience has shown that a filter with large grade medium supplied with a moderate amount of average town sewage builds up a fauna with several successful forms but, under other conditions, the fauna tends to be limited to very few species. It has been suggested that the strength of the sewage is the chief cause of limitation (Lloyd 1945), whilst the method of delivery, the medium used and the way in which the bed is constructed may all have some measure of responsibility (Lloyd, Graham & Reynoldson 1940). On the other hand, it has been held that the loading of the filter is the overriding factor (Tomlinson & Stride 1945).

The present studies were made at the Bradford Corporation's works at Esholt and North Bierley. The beds here provide a variety of conditions, both small and large medium with strong sewage and small medium with weak sewage. They were chosen as contrasting with the Knostrop works at Leeds where the medium is large and the sewage relatively weak. The fauna of Knostrop has already been described in detail (Lloyd 1935, 1937). The sewage passing to the Esholt works contains a large proportion of industrial wastes and is characterized by its high biochemical oxygen demand and its low pH. The beds are rectangular in shape, flush with the ground and 6 ft in depth. They are fed from travelling distributors at a rate of 75 gal per sq. yd per day. Hard coal of $\frac{3}{4}$ in. grade is employed as the filtering medium in most of the beds but, in recent years, five acres of this has been replaced by sandstone and river pebbles of 2-2$\frac{1}{2}$ in. grade. The fungus *Fusarium aqueductum* (Ascomycetes) is found on both types of medium and is evidently suited to the acid conditions (Butcher 1932). The growth is especially heavy during the winter months when there is a danger of its blocking the filters. There is also a growth of the alga *Phormidium* (Cyanophyceae) on the pebble beds but not on the coal. In late autumn and winter, this forms a thick leathery growth but

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diminishes to a mere trace in the late spring. The North Bierley works are much smaller than Esholt and deal with a weaker, mainly domestic sewage. Hard coal of $\frac{3}{4}$ in. grade is in use as a filtering medium throughout. The beds are again rectangular and the rate of dosage is 120 gal per sq. yd per day. Neither *Fusarium* nor *Phormidium* appears on the North Bierley beds.

Particular attention was given to the following species of sewage flies. Some predominate in the fauna whilst others are of peculiar interest:

Psychodidae	*Psychoda severini* Tonn.
	P. alternata Say.
Chironomidae	*Hydrobaenus* (= *Spaniotoma*) (*Limnophytes*) *minimus* Mg.
	Metriocnemus hygropetricus Kief. (= *longitarsus* Goet.)
Ephydridae	*Scatella silacea* Loew.
Anisopidae	*Anisopus fenestralis* Scop.

The output of flies from the beds was used as an index of the population and was measured by trapping emerging flies in shallow wooden trays of 1 sq. ft area pierced by a central hole over which rests a glass jar containing an inverted paper cone (Lloyd 1935). Corrugated paper lined the jars to afford resting places for the insects. Around the base of the trap was a rubber flange 2 in. wide, which was covered with medium when the trap was placed on the bed. This helped to prevent surface migration in and out of the tray. Four such traps were used on the Esholt beds (two on the coal, two on the pebbles) and one at North Bierley. The jars were changed twice weekly and the traps moved to fresh sites once weekly. The trapped flies were chloroformed, shaken out on to squared paper and counted. The trap operates on the principle that the flies, on emergence, seek out the light and so enter the jar. There is no stimulus to return once they are inside. *Psychoda alternata*, however, is an insect which prefers dusky places so that the numbers in the jar are not a reliable indication of its emergence. The number of flies found beneath the trapping trays provided an estimation of population in this case.

TRAPPING RECORDS

(*a*) *Psychodidae*

Three species of Psychodidae are known to breed in sewage filter beds, *Psychoda alternata*, *P. severini* and *P. cinerea*. Only the first two have been encountered in the present survey although it is known that *P. cinerea* does occur in the district, at the Huddersfield works.

P. alternata is probably the best known of all the sewage flies and is found in almost all filter beds. It is easily distinguished from the other species of *Psychoda* by its more hairy aspect and by the presence of six black spots on each wing. The records of emergence made at North Bierley and Esholt show it to be abundant in all beds, but certain definite differences can be seen in its seasonal incidence on the various filters (Fig. 1). All incidence curves conform to a main pattern.

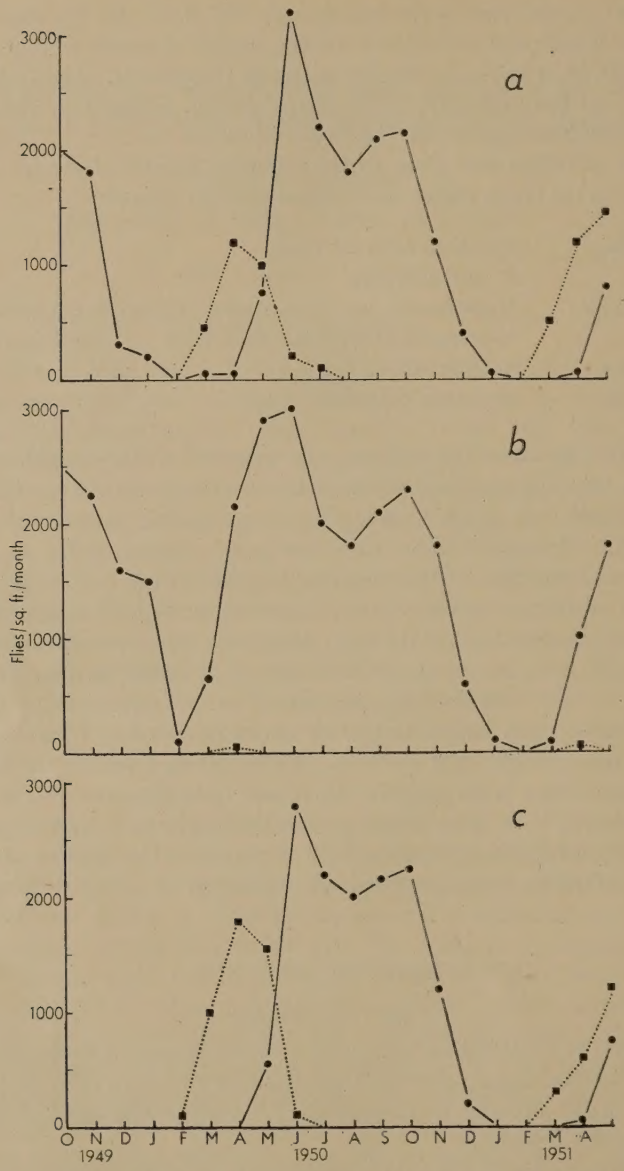

Fig. 1. Average weekly catches of *Psychoda* on *a*, Esholt pebble beds; *b*, Esholt coal beds; *c*, North Bierley coal beds. ●——● *P. alternata*; ■.....■ *P. severini*. No observations were made at North Bierley before February 1950.

There is a reduction in abundance in the autumn, and numbers remain at a low level during the winter. There is then a spring recovery followed by a double peak in the summer. The curves for the Esholt pebble beds and the North Bierley coal beds correspond closely, but they differ from the curve for the Esholt coal beds, which shows a much shorter winter depression and a more rapid spring recovery.

Psychoda severini, unlike *P. alternata*, is parthenogenetic. The male has never appeared in collections made on the filter beds although it has been reported from Belgium (Tonnoir 1922). It is readily distinguished from *P. alternata* by its reduced hairiness and absence of wing-spots, and from *P. cinerea* by the form of the anten-

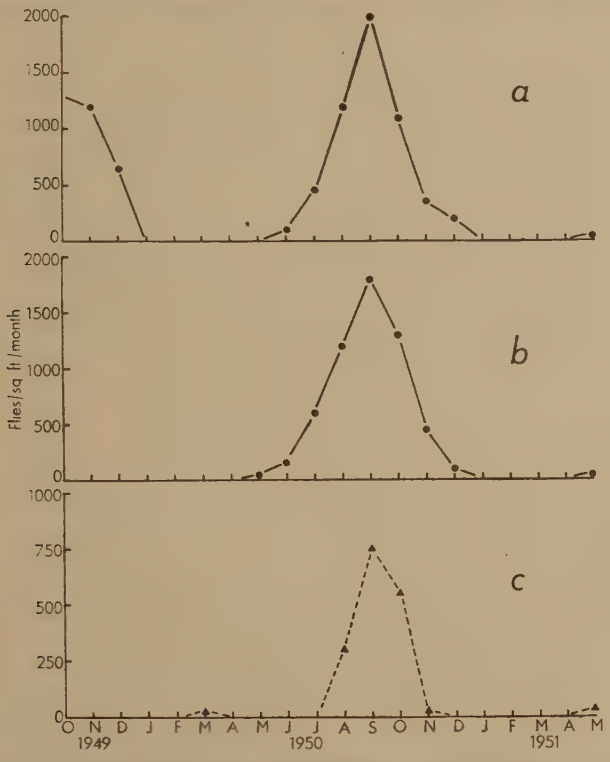

Fig. 2. Average weekly catches of *a*, *Hydrobaenus minimus* on the Esholt pebble beds; *b*, *H. minimus* on the North Bierley coal beds; *c*, *Scatella silacea* on the Esholt pebble beds.

nal tip. Fig. 1 shows that the pattern of incidence is roughly the same for all beds. The numbers of *P. severini* are low during the autumn and early winter but in March the fly becomes abundant and remains so throughout the spring. By June, however, numbers are once again decreasing and they remain at a low level until the following spring. The incidence curves for the Esholt pebble beds and the North Bierley beds are similar not only in shape but in the actual figures for the weekly catches. *P. severini* is much less abundant on the Esholt coal filters, the maximum weekly catch there being only 50 flies per sq. ft.

(*b*) *Chironomidae*

Two species of the genus *Hydrobaenus* are known to breed in sewage filters, *Hydrobaenus* (*Limnophytes*) *minimus* and *Hydrobaenus* (*Orthocladius*) *perennis*. The latter has not been encountered at Esholt and North Bierley although it does occur in the nearby works at Knostrop and Rodley. *H. minimus* is a tiny black midge which may rival *Psychoda alternata* in abundance in some beds. The males form mating swarms a short distance from the ground, these swarms being necessary for successful mating. They require calm weather for their formation and are soon dispersed by wind (Gibson 1945). The incidence curves for the Esholt pebble beds and the North Bierley filters are again similar in pattern (Fig. 2). Each

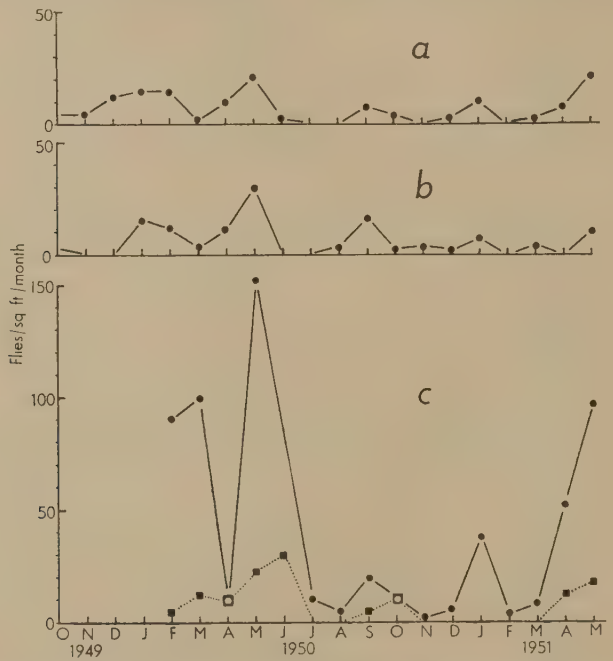

Fig. 3. Average weekly catches of *Metriocnemus* on *a*, Esholt pebble beds; *b*, Esholt coal beds; *c*, North Bierley coal beds. ●——● *M. hygropetricus*; ■.....■ *M. longitarsus*.

shows a rapid rise in abundance during the late spring and summer to a single peak in September. Numbers fall during the late autumn equally rapidly and the adults are virtually absent from the beds during the winter months. No *Hydrobaenus minimus* were trapped on the Esholt coal beds during the present survey although it was found breeding here in small numbers in 1934 (Lloyd, unpublished).

Two species of *Metriocnemus* are commonly found in sewage filter beds, *M. hygropetricus* and *M. hirticollis*. These midges are considerably larger than the tiny *Hydrobaenus minimus* and are further distinguished by having macrotrichia on the wings. The males of the two species are hardly distinguishable from one

another but the female of *Metriocnemus hygropetricus* is black while that of *M. hirticollis* is fawn-coloured. Accordingly only the figures for females are given in the trapping records (Fig. 3). The patterns of incidence for *M. hygropetricus* are similar in all three beds. Each shows a peak in May with subsidiary peaks in January and September. However, the numbers at North Bierley are considerably higher than those at Esholt. The abundance, in all cases, is much less than that of the *Psychodas* and *Hydrobaenus minimus*. *Metriocnemus hirticollis* has not been trapped on either the pebble beds or the coal beds at Esholt. It does occur at North Bierley but is less common than *M. hygropetricus*. Its maximum occurs in June, one month later than that of the related species.

(*c*) *Ephydridae*

Scatella silacea Loew is the only species of Ephydridae recorded in the present survey. Its incidence, habits and development have already been described in detail (Terry 1952). *S. silacea* was taken only from the Esholt pebble beds where its incidence curve showed a maximum in September with a small subsidiary peak in May (Fig. 2*c*).

(*d*) *Anisopidae*

No *Anisopus fenestralis* have been trapped at Esholt or North Bierley although the fly is abundant at other works in the district (Knostrop, Rodley and Oakenshaw). The Knostrop and Rodley works are ten and three miles respectively from Esholt, but the Oakenshaw plant is barely 200 yd from the North Bierley beds.

DISCUSSION

The most striking feature of the trapping records is the virtal absence of *Psychoda severini* and *Hydrobaenus minimus* from the Esholt coal filters although both are abundant in the Esholt pebble beds and the North Bierley coal filters. The absence of these flies from the coal beds cannot be correlated with the strength of sewage as they are numerous in the pebble beds which receive the same effluent. It cannot be attributed to the size of the medium as both species are abundant in the small coal at North Bierley. Further, the explanation cannot lie in the method of working the beds as all the Esholt filters are treated alike. However, a combination of the two factors, sewage strength and size of the medium, may produce conditions which will account for the distribution.

The small coal medium holds up accumulations of film and other solid matter more readily than does the large pebble medium. Thus the heavy growth of film produced by the strong Esholt sewage severely limits the air spaces in the coal medium. The effect is not as serious in the pebble medium as solid matter is more easily washed through the beds. At North Bierley the beds remain fairly open although the medium is of small coal. This may be due in part to the weaker sewage resulting in less growth of film and also to the scouring activities of the Enchytraeid worm *Lumbricillus lineatus* Mull. This worm is abundant at North Bierley but is rarely seen at Esholt.

The larva of *Hydrobaenus minimus* respires through the body surface and must

have access to air or be in an environment rich in dissolved oxygen. Such conditions do not exist in the Esholt coal beds. The sewage is devoid of dissolved oxygen and the air spaces in the medium are largely blocked. The size of the effective air spaces is greater in the pebble beds and the *H. minimus* larvae have better access to atmospheric oxygen. The same holds for the North Bierley coal beds for here there is a reduced growth of film. The virtual absence of *Psychoda severini* from the Esholt coal beds may be explained in a similar manner. The larva of this fly is a sturdy form and is incapable of elongation under very wet conditions. *P. severini* is excluded from very wet, foul environments in which *P. alternata* flourishes (Satchell 1947). The combination of small medium and heavy growth of film leads to such semi-fluid conditions arising in the Esholt coal filters whereas the pebble beds and the North Bierley coal filters are better drained.

The incidence curves of *P. alternata* on the Esholt pebble beds and the North Bierley coal filters (Fig. 1*a*, *c*), are similar in pattern and correspond closely to the curve obtained for large medium beds treated with a relatively weak sewage (Lloyd 1937). *P. alternata* is rarely found during the early part of the year and *P. severini*, with its lower 'threshold of development', is the dominant fly. However, as the bed temperatures rise in May, the lower 'thermal constant' of *P. alternata* gives it the advantage and it becomes dominant. In contrast to conditions at North Bierley and the Esholt pebble beds, the spring recovery of *P. alternata* in the Esholt coal beds is evident by April, and in 1950 February was the only month in which the population reached a really low level.

This early abundance of *P. alternata* in small grade medium beds, when observed previously, has been explained on the grounds that the small medium excluded certain competing species (Lloyd 1944, Hawkes & Jenkins 1951). It is unlikely that the distribution at Esholt can be explained in these terms as all beds carry a heavy growth of film throughout the spring and there would appear to be no shortage of food. Seemingly, the strong sewage and the small medium produce conditions which, if not carried to excess, are directly favourable to the development of *P. alternata*. These conditions may be in part a temperature effect. No continuous records of bed temperature have been made but three measurements in January 1951 showed the temperature at a depth of 1 ft to be 2·2·5° C higher in the coal beds than in the pebbles. This may be the result of less effective ventilation in the coal beds whereby the heat of vital processes are retained more readily than in the open pebble beds and North Bierley filters. The effect of these higher temperatures would be to enable *P. alternata* to begin its development at an earlier date.

Metriocnemus hygropetricus is more numerous in the North Bierley filters than in those at Esholt and no *M. hirticollis* have been trapped on the Esholt beds. Little can be said about these results other than, in general, they support the idea that *Metriocnemus* prefers clean, lightly-loaded filters.

The limitation of *Scatella silacea* to the Esholt pebble beds has been discussed in an earlier paper (Terry 1952). The distribution of the fly may be correlated with the growth of *Phormidium* which occurs only on the pebble beds.

The absence of *Anisopus fenestralis* from the coal beds at Esholt and North Bierley appear to support the idea that small grade medium is unsuitable for the development of this fly (Tomlinson & Stride 1945, Hawkes & Jenkins 1951). The open medium of the Esholt pebble beds may yet be invaded successfully, or alternatively the Esholt sewage may be unsuitable for *A. fenestralis*.

Seemingly then there are cases where neither the strength of the sewage nor the size of the medium is sufficient in itself to limit the bed fauna, yet a combination of the two factors may do so quite drastically. Experience in sewage works practice has shown that a filter with large grade medium fed with a moderate amount of average town sewage naturally acquires a mixture of successful forms. It can now be said that small grade medium beds fed with weak sewage and large medium beds fed with strong sewage also acquire a mixed fauna. Where a small grade medium is fed with a strong sewage, as in the case of the Esholt coal filters, it is neither the medium size nor the sewage strength *per se* which limits the fauna, but a combination of the two. However, the strength of the sewage may over-ride all other factors. The very strong sewage treated at the Huddersfield works excludes almost all forms but the very resistant *Psychoda alternata*.

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SUMMARY

1. The relations of the bed medium of sewage filters and the flies breeding in them have been investigated at various works in the West Riding of Yorkshire. The beds chosen showed different combinations of size of medium and sewage strength.

2. *Psychoda severini* and *Hydrobaenus minimus* are abundant in small medium fed with weak sewage and large medium fed with strong sewage but absent from small medium fed with strong sewage. This absence is probably due to the combined effect of the sewage and the medium producing wet and badly aerated conditions.

3. *Psychoda alternata*, however, flourishes in such beds and has a longer period of abundance than elsewhere, possibly due to the higher bed temperatures found here.

4. These studies support the idea that species of *Metriocnemus* prefer clean, lightly loaded filters and also that small grade medium is unsuitable for the development of *Anisopus fenestralis*.

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THE ABUNDANCE AND DISTRIBUTION OF PROTURA IN GRASSLAND

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(With 1 Figure in the Text)

INTRODUCTION

The Protura, first described by Silvestri (1907), are generally regarded as uncommon insects. Early records, based upon the discovery of few or even single specimens, described them as occurring in damp situations where decomposing organic matter, such as decomposing leaves, moss, and rotting tree stumps, was abundant (Berlese 1909, Rimsky-Korsakov 1911, Prell 1913, Williams 1913). Berlese (1909) emphasized their susceptibility to desiccation. Following a preliminary investigation of several habitats Tuxen (1931) tentatively suggested that the abundance of Protura may be affected by the pH of the habitat, for he found them more abundant in the more acid habitats. Strenzke (1942) studying their distribution in N.W. Germany found them principally in moist humic soils associated with lakeside forests. The most abundant species, *Eosentomon armatum* Stack, occurred chiefly in neutral or slightly alkaline soils though it tolerated a range of acidity. The less abundant *Acerentomon doderoi* Silvestri on the other hand occurred chiefly in slightly acid soils. Strenzke considered, however, that organic matter was the principal factor affecting their distribution.

There have been few records of the occurrence of Protura in agricultural soils and it has been supposed that their abundance in forest soils and scarcity in agricultural soils was due to their high moisture and organic matter requirements (Strenzke 1942, Kühnelt 1950). However, Salt, Hollick, Raw & Brian (1948) found 221 specimens in twenty soil samples, each 4 in. diameter, 12 in. deep, taken from a permanent pasture in Cambridgeshire—much the highest population hitherto recorded from grassland. The data recorded below were collected during a study of the arthropod fauna of the soil of the Park Grass plots at Rothamsted. During this study Protura were found to be so numerous and their distribution was so striking that it seemed desirable to give a separate account of them.

SITES AND METHODS

The Rothamsted Park Grass plots were laid out in 1856 to study the effect of various manurial treatments on hay production. The site chosen for the experiment was a field which had been under permanent grass for several centuries and which appeared to have a uniform vegetation. The manurial treatments were of

five types: (1) no manure, (2) organic manures, (3) nitrogenous manures, (4) mineral manures, (5) mixed mineral and nitrogenous manures, and with minor modifications these have been applied annually to their respective plots since 1856. Since 1903 one half of each plot has been limed every fourth year and the other half has remained unlimed. Until 1872 the field was cut for hay each year and the aftermath grazed by sheep. Since then the aftermath has also been cut for hay and no stock has been admitted. The treatments have effected great changes in the vegetation of the plots and in certain physical and chemical properties of the soil. In so far as they now provide markedly contrasted habitats in the same soil type and with the same climate the plots offer a unique opportunity for studying the distribution of soil arthropods, as it is reasonable to assume that marked differences in the population of the plots have resulted from the changes induced by the treatments.

Nine plots representing the various types of vegetation and soil conditions were chosen for study (Table 1). In October 1950 ten soil samples, each comprising a cylinder of soil 2 in. diameter and 9 in. deep, were taken from each plot; five from the limed section and five from the unlimed section. Within each section the samples were taken at random and before taking each sample the vegetation was cut off at ground level. The arthropods were extracted from the samples by the flotation process used by Salt *et al.* (1948), and described in detail by Salt & Hollick (1944), except that the fine sieve on which the arthropods were retained had a regular square mesh of 0·1 mm. It is not claimed that all the Protura were recovered by this method for clearly there would be some loss of specimens less than 0·1 mm. diameter. Subsequent measurements of the first stage larvae of *Proturentomon minimum* (Gisin), the dominant species collected, show it to be about 0·09 mm. diameter so that recovery of this stage would be incomplete. The numbers recorded do not therefore represent the total population. However, the possibility of loss was the same for all the samples and does not therefore invalidate a comparison of the populations of the different plots.

RESULTS

The numbers of Protura collected from the ninety soil samples are shown in Table 1. 1425 Protura were collected, 1217 from the limed sections and 208 from the unlimed sections. Of the total specimens 1296 have been identified, 1101 as *Proturentomon minimum*, and the remaining 195 as a species of *Eosentomon*, probably *E. armatum*. Mature and immature stages of both species were present. These results are summarized in Table 2.

In considering the distribution of the two species it is evident from the data in Table 1 that they are not distributed at random. The numbers found in individual samples within the same section vary greatly and indicate that the Protura tend to occur in groups. Treating the limed and unlimed sections as two separate groups, some measure of the degree of aggregation has been obtained as follows: each individual sample count (n) has been converted to a logarithm, $\log_{10}(n+1)$,

and the logarithmic mean for each section has been calculated. The deviation of each sample count from the logarithmic mean of its section has then been obtained and these deviations have been plotted in Fig. 1. The symmetry of the two frequency distributions is evidence that the logarithmic transformation was appropriate. The standard deviation for each group is 0·36 and it can be seen that for both groups about 60% of individual counts deviate from the log mean by $\pm 0{\cdot}8$ and about 80% by $\pm 0{\cdot}4$. In this respect the two groups are essentially similar. This means that the Protura are aggregated in such a way that, when sampled, about 60% of individual sample counts fall within the range one-half to twice the geometric mean of the population and about 80% within the range two-fifths to two-and-one-half times the geometric mean (antilog 0·3 = 2, antilog 0·4 = 2·5). Moreover, the degree of aggregation, appears to be independent of the population density.

The preponderance of Protura in the limed sections of the plots suggests that

Table 1. *Numbers of Protura collected from five soil samples from each plot section*

		Limed Section						Unlimed Section					
Sample		1	2	3	4	5		1	2	3	4	5	
	Manurial Treatment						Total						Total
Plot 1	N_1	1	22	154	14	7	198	4	13	0	2	1	20
3	None	7	33	62	25	8	135	3	3	1	1	3	11
4	N_3, P	3	1	5	8	2	19	0	0	0	0	0	0
7	P, K, Na, Mg	5	15	11	22	1	54	22	0	2	1	0	25
8	P, Na, Mg	8	14	34	42	11	109	6	5	11	10	5	37
11	N_3, P, K, Na, Mg	0	0	0	0	0	0	0	0	0	0	0	0
13	Dung+fish guano	9	4	10	12	23	58	26	1	1	2	4	34
14	N^*_2, P, K, Na, Mg	16	6	6	20	1	49	0	12	2	9	1	24
17	N^*_1	74	81	256	129	55	595	17	3	3	12	22	57
					Total		1217					Total	208
												Grand total	1425

Manurial treatments (*amounts per acre*):

N_1, N_2, N_3	2, 4, 6 cwt Sulphate of ammonia	N^*_1, N^*_2	2½, 5 cwt Nitrate of soda
P	3½ cwt Superphosphate	K	4½ cwt Sulphate of potash
Na	1 cwt Sulphate of soda	Mg	1 cwt Sulphate of magnesia
Dung	14 tons every 4th year: 1905, 1909, etc.	Fish guano	6 cwt every 4th year: 1907, 1911, etc.

Limed sections receive 2000 lb ground lime per acre every 4 years.

their distribution is affected by the conditions induced by liming. Two soil properties which liming is known to affect are exchangeable calcium and pH. These properties are also affected by the manurial treatments, e.g. the repeated application of sulphate of ammonia lowers the pH. For this reason it is appropriate to consider the plot sections as a series rather than as two groups. The relevant data, based upon analyses of representative soil samples, are given in Table 3 together with the correlation coefficients between these two factors and the number of each species of Protura. These and other analyses are based on a logarithmic transformation of the numbers of Protura from each section. *Proturentomon minimum* is strongly correlated with exchangeable calcium and pH; in both cases the value of the correlation coefficient exceeds the 1% level of significance. *Eosentomon* sp. is correlated with exchangeable calcium at the 5% level but not with pH.

As liming and the manurial treatments have considerably changed the vegetation of the plots the relationship between the abundance of Protura and the abundance of certain plant species may be considered. The botanical composition of the vegetation of the plots has been studied over a period of years by members

Table 2. *Numbers of* Proturentomon minimum *and* Eosentomon *sp. identified from Protura collected from each plot section*

	Plots									
	1	3	4_2	7	8	11_1	13	14	17	Total
Limed Sections										
Proturentomon minimum	182	116	1	37	99	0	39	38	517	1029
Eosentomon sp.	11	13	9	11	7	0	9	5	23	88
Total determined	193	129	10	48	106	0	48	43	540	1117
Total in samples	198	135	19	54	109	0	58	49	595	1217
Unlimed Sections										
Proturentomon minimum	3	2	0	18	0	0	17	2	30	72
Eosentomon sp.	13	8	0	0	26	0	17	21	22	107
Total determined	16	10	0	18	26	0	34	23	52	179
Total in samples	20	11	0	25	37	0	34	24	57	208

of the Botany Department at Rothamsted and detailed information exists about the relative abundance of the numerous plant species found on the plots. Protura were most abundant on the limed section of plot 17 and for the present purpose only the dominant grasses of this section have been considered. They are *Helicto-*

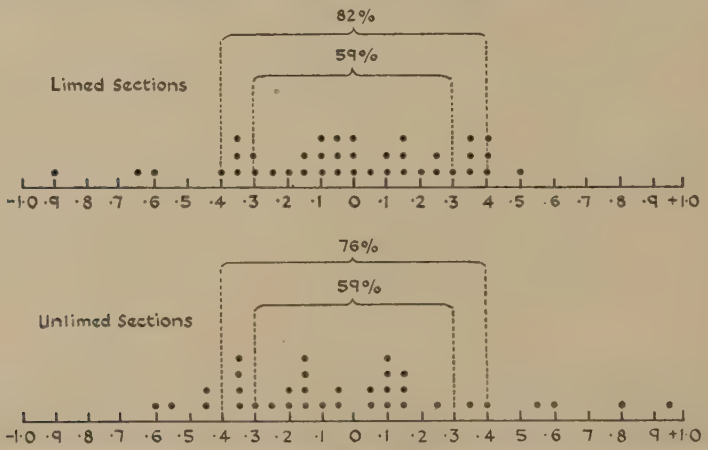

Fig. 1. Numbers of Protura per sample $\log_{10}(n+1)$. Frequency distributions of deviations from log. means.

trichon pubescens (Huds.), *Dactylis glomerata* L. and *Festuca ovina* L. *Trisetum flavescens* (L.) and *Festuca pratensis* Huds. also occur on some of the plots and have been included in the estimates for the other species of the genus. The relevant data and correlation coefficients are given in Table 3. *Proturentomon minimum* is strongly correlated with *Helictotrichon* and *Trisetum* and is also correlated with *Dactylis glomerata* but not with *Festuca*. *Eosentomon* sp. is not significantly correlated with any plant species.

DISCUSSION

The data presented, though admittedly incomplete, represent the greatest populations of Protura so far recorded from grassland. Indeed 256 specimens from a single sample from the limed section of plot 17 probably represents the greatest concentration recorded from any habitat. As several of the plots where Protura were numerous typify permanent grassland under normal management, it is clear that the Protura as a group must be considered as a significant part of the arthropod fauna of such grassland and in no way limited to forest soils. The marked difference in abundance of the two species confirms the earlier observations of Strenzke that species may have different requirements or differ in their response to environmental changes.

Table 3. *Correlation between numbers of Protura and soil and vegetative factors (logarithmic transformation)*

Plot	*Protur-entomon minimum*	*Eosentomon* sp.	Ca^{++}§	pH	% *Helicto-trichon* + *Trisetum*	% *Dactylis*	% *Festuca*†
1·1	2·26	1·08	14·5	6·8	13·8	18·3	15·4
u	·60	1·15	2·8	3·4	0·2	3·2	15·6
3·1	2·07	1·15	16·8	7·0	14·6	3·3	4·1
u	·48	·95	9·3	4·8	2·9	4·5	16·6
4·1	·30	1·00	15·1	5·6	0·3	0·3	57·4
u	·00	·00	0·7	3·3	0·0	0·0	35·3
7·1	1·58	1·08	14·0	5·3	7·7	13·2	4·3
u	1·28	·00	5·1	4·4	2·1	15·7	4·9
8·1	2·00	·90	18·2	6·8	13·4	5·6	9·0
u	·00	1·43	9·4	4·8	2·4	12·6	5·6
11·1	·00	·00	5·1	4·0	0·0	4·9	0·4
u	·00	·00	1·9	3·2	0·0	0·0	0·0
13·1	1·60	1·00	15·0	6·8	0·4	21·5	0·9
u	1·26	1·26	4·7	4·4	0·0	9·1	4·0
14·1	1·59	·78	15·3	6·6	5·8	13·6	13·3
u	·48	1·34	9·6	5·4	1·6	14·2	0·0
17·1	2·71	1·38	15·9	7·1	22·0	21·1	23·1
u	1·49	1·36	11·2	5·2	1·6	25·4	9·4
'r'	*P. minimum*		+·708**	+·805**	+·810**	+·580*	−·126
'r'	*Eosentomon* sp.		+·551*	+·012	−·014	+·443	+·006

§ Exchangeable calcium Ca^{++} expressed as milli-equivalents/100 g.
† *F. ovina* plus *F. pratensis*.
** Significant at 1% level; * at 5% level.

Other soil arthropods such as wireworms (Salt & Hollick 1946) and mites and Collembola (Macfadyen 1953) have been shown to be aggregated in their distribution. Indeed the results of population studies suggest that some degree of aggregation is typical of soil arthropods. As the soil is a heterogeneous medium some aggregation may arise from the localization of favourable conditions, such as food supply. However, the degree of aggregation exhibited by the Protura appears to be similar for different population densities which suggests that it may be due to some vital characteristic such as reproductive rate. It may be that some soil organisms have limited powers of dispersal and that dispersal from centres of reproduction is relatively slow.

In considering the significance of correlations between the abundance of Protura and soil and vegetative factors one is handicapped by an almost total absence of

information about their habits. It is not known with certainty whether Protura are predaceous or phytophagous and in the absence of such information it is impossible to assess the significance of such correlations as that between *Proturentomon minimum* and the abundance of *Helictotrichon* and *Trisetum*. Moreover the soil and vegetative factors are themselves closely correlated (these grasses are known to respond to liming), and much more data would be required before the interrelationships could be successfully analysed by partial correlations. Until there is more information about the biology of Protura and until their distribution in other types of grassland and in other soils has been investigated little further progress can be made.

There is one further point for consideration. With the exception of Salt *et al.* previous investigators have extracted Protura from soil or litter samples by some modification of a Berlese funnel. This technique appears to be more suitable for litter than for soil samples, for heavy soils tend to bake on drying and small organisms which are susceptible to desiccation may be trapped in the sample. Attempts to extract living Protura from Park Grass soil using a Berlese funnel have been relatively unsuccessful. It may be that the high populations recorded when the flotation method has been used are due in part to the greater suitability of this technique.

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SUMMARY

1. Using a flotation method 1425 Protura were extracted from ninety soil samples taken from selected Park Grass plots at Rothamsted in October 1950. Of these 85% were identified as *Proturentomon minimum* (Gisin), the rest as a species of *Eosentomon*, probably *E. armatum* Stack.

2. The Protura were aggregated in such a way that the majority of individual sample counts fell within the range one-half to twice the geometric mean of the population. The degree of aggregation appeared to be independent of the population density.

3. Their distribution was associated with conditions induced by liming. Both species were correlated with exchangeable calcium. *Proturentomon minimum* was also correlated with soil pH and the abundance of *Helictotrichon*, *Trisetum*, and *Dactylis* spp. The significance of their aggregation and distribution is briefly discussed.

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SOME OBSERVATIONS ON THE EFFECTS OF WATER INFLOW AND OUTFLOW ON THE PLANKTON OF SMALL LAKES

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(With 7 Figures in the Text)

INTRODUCTION

Of the factors which determine the abundance of the plankton in a lake it is believed that the flow of water through the lake may at times be of over-riding importance. In fact many small lakes may be regarded as parts of river or stream systems in which the flow of water has been temporarily impeded. Studies of the plankton of flowing waters indicate that the quantity of their plankton is inversely proportional to the current speed (Brook & Rzòska 1954, Rzòska, Brook & Prowse 1955). The magnitude of the influence of the flow of water through a lake will depend on the volume of the lake, the extent of its catchment area and the amount of rainfall on this area. Thus the effect will be greatest in a small shallow lake with a large catchment area receiving high rainfall, and will become less significant the bigger the lake and the smaller the catchment area and rainfall. For purposes of comparison, a figure representing the replacement of water in a lake may be determined by dividing the volume of water contained in the lake by the amount of water passing through for a given period. This *replacement quotient* has been expressed in the following paper in days. Clearly, in any lake an increase in the standing crop of plankton will indicate that the rate of increase of the plankton is greater than the diluting effect of the replacement water, though the converse may not be true, for this may be due to the death of plankton. Hence the productivity of a lake with a rapid replacement of water may actually be greater than that of a lake with a slow replacement though standing crop estimates may suggest the contrary.

The effect of the flow through may, however, be modified by a number of factors. For example, although the annual rainfall on the catchment area is of prime importance, its incidence may also be significant. A short period of heavy rain will have a greater effect than the same amount of rain spread over a longer period. The topography, geology and vegetation of the catchment area will affect the speed of run-off and the proportion of the rainfall that actually runs into the lake. A number of small inlets bringing in the same amount of water as one large inlet may produce a very different result. The effect in lakes with inflowing streams opposite those flowing out will differ considerably from those with inflows near the outflow. Other morphological features of the lake, such as the size and distribution of islands and weed-beds may either confine or spread the inflowing water.

SITES AND METHODS

It has been observed, during the course of observations extending over a period of four years in four Scottish hill lochs, that the population density of the plankton tends to be highest and most stable in lochs with a high replacement quotient.

Table 1. *Some physical data relating to the lochs investigated*

	Volume (cu. ft. $\times 10^6$)	Estimated annual outflow* (cu. ft. $\times 10^6$)	Replacement quotient (days)
Loch Kinardochy	14·0	56·0	91
Loch Moraig	8·9	124·6	26
Loch Choin	18·2	431·0	16
Lochan an Daim	1·1	82·5	5

* This figure was calculated from the size of the catchment area and the annual rainfall at the loch, and was confirmed by measurement of the outflow. The increased amount (2½% per 100 ft) of rain falling on the higher ground around the lochs, and water lost by evaporation have been ignored.

Table 1 gives details of the volume, annual outflow and replacement quotient of these four lochs. The considerable difference in the calculated replacement quotient between Loch Kinardochy and Lochan an Daim will be noted. In view of

Fig. 1. *a*, Lochan an Daim; *b*, Loch Kinardochy.
Sampling stations: ■, phytoplankton; ●, zooplankton.

these differences detailed concurrent observations were made during the spring and summer of 1954 on the plankton and replacement of water in these two lochs to determine more precisely the influence of flow-through. In Loch Kinardochy (Fig. 1) which is forty-one acres in extent with a maximum depth of 30 ft and average depth of 8 ft, the inflowing water comes from many small drainage

channels. The loch has one small outflow in which a V-notch weir was built to enable accurate measurements of the rate of outflow to be made. Lochan an Daim, an artificial loch, is much smaller and shallower, and is situated some three miles north-west of Loch Kinardochy. It is about ten acres in extent with an average depth of $2\frac{1}{2}$ ft, and maximum depth of 4 ft. It has dense beds of aquatic macrophytes and numerous islands with considerable growths of *Phragmites communis* Trin. and *Carex rostrata* Stokes growing round and on them. There is a well-defined inlet burn which drains a large area of Schiehallion (3547 ft) while at the loch outflow there is a permanent concrete rectangular weir 8 ft in width. A continuous recording depth meter was set up in the loch to record the height of water passing over this weir.

In addition to these studies, measurements of replacement and plankton observations were made at the Pitlochry Reservoirs. These consist of two rectangular basins, the northern holding 1 250 000 gallons and the southern 750 000 gallons. Estimates of replacement in the two basins were determined by measuring the depth of water and current speeds in the inflow pipes. During the periods of observation at both lochs and at the reservoirs plankton samples were taken weekly and, over short periods, daily.

Both phyto- and zooplankton samples from the lochs and reservoirs were taken throughout these investigations from the surface only, previous studies over a long period having shown no significant differences in numbers with depth. Only in Lochan an Daim were there significant local differences in plankton density and these were more pronounced in the case of the zooplankton than for phytoplankton. Eight sites were accordingly sampled on each visit for zooplankton in this loch and three for phytoplankton (Fig. 1). Previous years' sampling of five widely separated sites in Loch Kinardochy had shown plankton distribution throughout this loch to be remarkably even and thus during the present study only three sites were sampled per visit for zooplankton and four for phytoplankton (Fig. 1). Owing to the fact that a boat could not be used on the Pitlochry Reservoirs, plankton samples from here were taken only from the jetty leading to the outflow pipes.

All phytoplankton samples were preserved in iodine and counted in 1 ml Naumann cells. Zooplankton samples were collected with a 5 litre Rodhe sampler and concentrated in the field by filtration through a fine wire gauze which fitted on to the end of the sampler. All the organisms in each sample were counted.

RESULTS OF MEASUREMENTS OF REPLACEMENT QUOTIENT

In Loch Kinardochy water levels fluctuated but little, even after heavy rainfall, and measurements of the rate of flow through indicated that during the period of these observations the replacement quotient varied from seventy days to more than a year (Fig. 2). In Lochan an Daim, however, the depth records show rapid changes in loch height and hence in the volume of the outflow, the replacement quotient varying between one and thirty days (Fig. 3). These changes show

clearly the river-like characteristics of this lochan with its well-defined periods of spate. A typical spate pattern is reproduced from one of the depth recorder charts in Fig. 4.

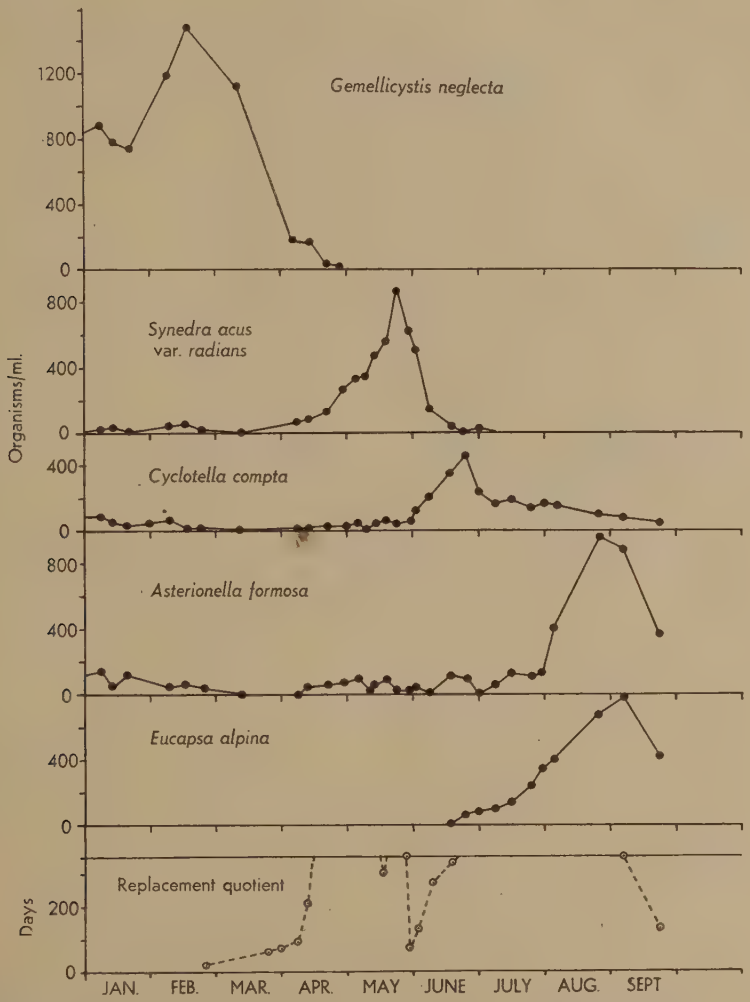

Fig. 2. Loch Kinardochy, 1954: seasonal variations of the principal phytoplankton species and the replacement quotient.

Measurements of the inflows to both basins of the Pitlochry Reservoirs show that their turnover was in general even more rapid than that of Lochan an Daim, their replacement quotient being never more than four days and averaging 2·5 days.

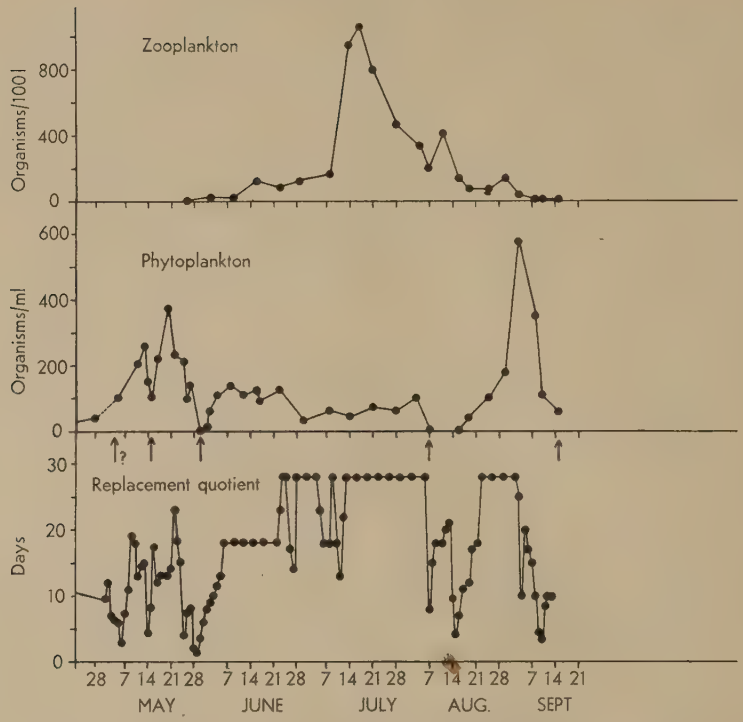

Fig. 3. Lochan an Daim, 1954; seasonal variations in plankton and replacement quotient. Arrows indicate spates which affected the plankton.

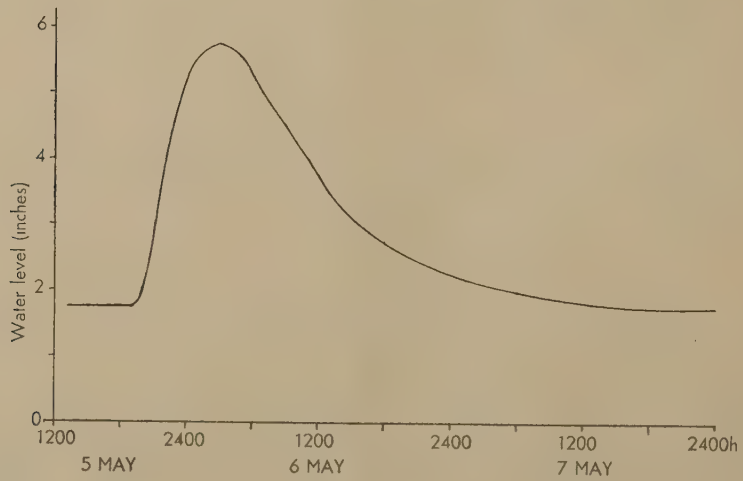

Fig. 4. Spate pattern on the depth recorder chart; Lochan an Daim, 5-7 May 1954

GENERAL BIOLOGICAL RESULTS

The plankton population of Loch Kinardochy is a comparatively stable one in which there is a clear successional pattern of species (Figs. 2, 6 and 7) and at no time have all species been observed to decrease in numbers simultaneously. Moreover, the plankton persists throughout the year in all open water sites, though considered as a whole it is least abundant in winter. Thus in this loch the factors controlling the growth and decline of planktonic organisms would seem to be mainly chemical and biological rather than physical, though of course light and temperature doubtless affect the broader seasonal changes which are observed.

In contrast to Loch Kinardochy there was plankton present in Lochan an Daim for only a comparatively short period of the year, and its appearance, particularly in the case of the zooplankton, seems to be associated with the persistence of a slow flow through, the replacement quotient being consistently greater than eighteen days before the zooplankton developed significantly. In the case of the phytoplankton the situation is less clear though this seems to be able to develop at a lower replacement quotient (probably greater than ten days) and even when conditions are comparatively unstable. Whilst infrequent sampling may have caused the effects of the first recorded spate (between 1 and 6 May) to have been missed, there were clear indications of washouts of phytoplankton following the spates of 14 and 28 May and again on 7 August. The final disappearance of both phyto- and zooplankton began in the first days of September when there was high rainfall which continued throughout that month and the next. During October 1954 there were periods when the estimated replacement quotient was less than one day. Previous years' observations have shown that for a considerable part of each year, usually between October and April, the open water of Lochan an Daim is devoid of plankton.

The consistently low replacement quotient observed in both basins of the Pitlochry Reservoirs seems to confirm that rapid replacement is inimical to plankton production, for throughout the period of observation only occasional plankton organisms were found. It will be remembered that the replacement quotient of both basins was never more than four days.

DETAILED OBSERVATIONS ON THE THE PHYTOPLANKTON

The seasonal changes in the density of the principal components of the phytoplankton of the oligotrophic Loch Kinardochy (see Fig. 2) indicate that the variations observed show no clear association with the variations in the replacement quotient of the loch. The successional pattern of species in the loch is comparable with that of a large, stable loch in which the decline in numbers following a maximum is usually the result of nutrient depletion or, on occasions, parasitism (Canter & Lund 1948, 1951). It is of interest to record in this latter connection that infection by the fungal parasite *Rhizophidium fulgens* Canter probably caused the death in early April of the large *Gemellicystis neglecta* Teiling (Skuja) population which had been present throughout the previous winter.

Unlike Loch Kinardochy, the distribution of phytoplankton in Lochan an Daim shows considerable differences in different localities within the lochan. The phytoplankton first appeared in those areas sheltered by the islands, and throughout the period of its presence it was usually more abundant in these localities than in open water sites. Furthermore, the effects of spates were most devastating to the plankton of the open water which was occasionally removed completely while some organisms still remained amongst the islands and near weed beds. It seems probable that the replenishment of the open water plankton after such spates was from these localities. Lochan an Daim has an unusual phytoplankton being dominated by *Dinobryon sociale* var. *americanum* (Brunn.) Bachn., usually from April to July and by *Chroomonas acuta* Ütermohl and *Dinobryon sociale* var. *americanum* from August until its final disappearance in September or October. The planktonic diatoms *Synedra acus* var. *radians* (Kütz) Hust., *Cyclotella comta* (Ehr.) Kütz., very rare colonies of *Asterionella formosa* Hass. and some Chlorophyceae and Cyanophyceae are also present from spring to autumn, but these have never been recorded in numbers greater than 1 or 2 per ml. It seems possible, since chemical analyses have shown nothing unusual in the concentration of nutrients in the water of this lochan, that the fuller development of diatoms, Chlorophyceae and Cyanophyceae, is prevented initially by the considerable flow of water through the lochan. By the time this is reduced, their growth and that of *Dinobryon* is limited by lack of nutrients, which are taken up by the very dense growths of aquatic macrophytes and associated algal epiphytes that develop in early summer. Thus it seems that only rapidly reproducing species and possibly only species with low nutritional requirements can succeed in lochs with low replacement quotients. In this connection it is of considerable interest to compare the phytoplankton of Lochan an Daim with that of Loch Moraig which, though chemically and biologically similar, has a much higher replacement quotient (Table 1 and Fig. 5). Although the same species of phytoplankton are present in both, only in Loch Moraig with its higher replacement quotient does a complete plankton spectrum, with periods of diatom and cyanophycean dominance, in addition to the considerable maxima of *Dinobryon* and *Chroomonas*, develop. Observations in 1953 (Fig. 5) showed that the maxima of *Dinobryon* in both lochs occurred in late April, but in Lochan an Daim it appeared much later and disappeared sooner than in Loch Moraig. Furthermore in Loch Moraig its decline was accompanied by an increase in the population density of *Synedra acus* var. *radians*, to be followed later by *Cyclotella* spp. Thus it may be said that differences in the rate of replacement produce qualitative as well as quantitative differences in the plankton.

DETAILED OBSERVATIONS ON THE ZOOPLANKTON

In the Pitlochry Reservoirs the only planktonic crustacean present was *Daphnia hyalina* var. *lacustris* Leydig and this variety occurred spasmodically and only in very small numbers.

The zooplankton of Lochan an Daim is dominated by *D. hyalina* var. *lacustris*

with *Diaphanosoma brachyurum* (Liéven) appearing in small numbers later in the year. Though *Daphnia* was first found to be present on 26 May (see Figs. 3 and 7), it did not become numerous until 14 July and attained its maximum density of 1300 individuals/100 l. three days later, on 17 July. This maximum consisted

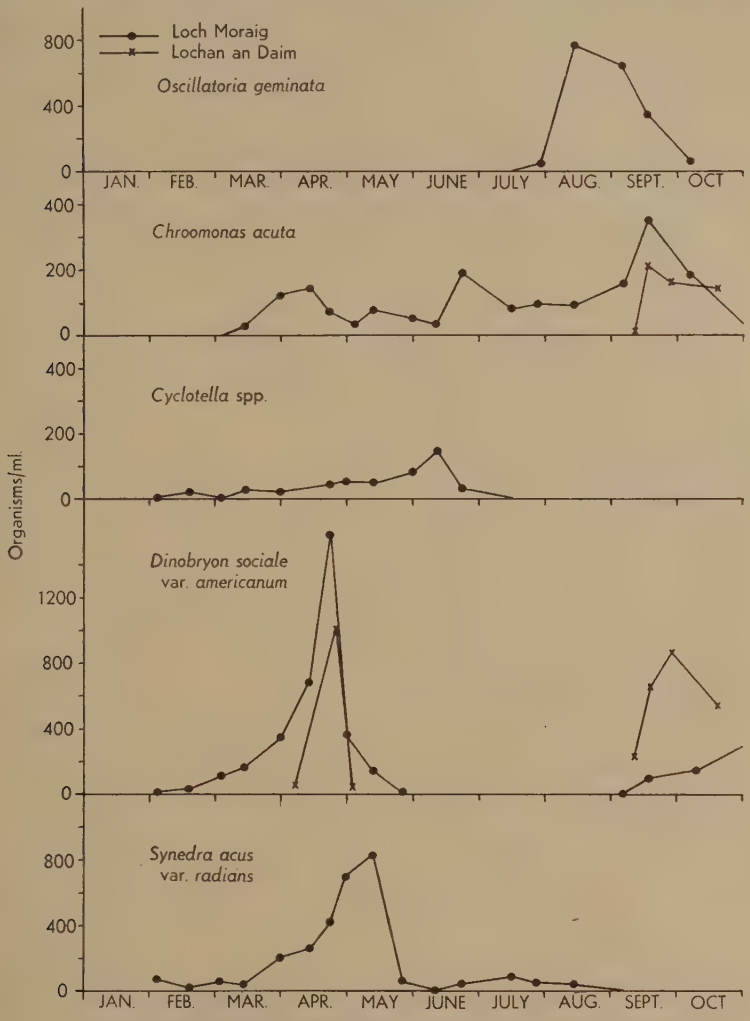

Fig. 5. Loch Moraig and Lochan an Daim, 1953: seasonal variations of the principal phytoplankton species.

almost entirely of young stages which reached maturity, with the appearance of ovigerous female adults and further young stages, some two to three weeks later. There were indications early in August that, as in previous years, a second maximum was about to be produced. However, a period of high water levels ensued

and only small numbers appeared. The period of higher replacement quotient which followed this apparent washout produced a small, short-lived increase in numbers which included a proportion of ephippial females. Finally, further high water levels in the middle of September removed all save occasional individuals.

The monospecific character of the zooplankton of Lochan an Daim (and the Pitlochry Reservoirs) may as in the case of the phytoplankton be the result of their comparatively rapid replacement, since Loch Moraig, which is biologically and chemically similar but has a much higher replacement quotient, has a zooplankton characterized when fully developed by large numbers of *Daphnia* and *Cyclops*. It is instructive in this connection to compare the species list of Lochan an Daim with that for Loch Moraig (see Table 2). Although most species are common to both localities it seems significant that only occasionally do individuals of species other than *Daphnia hyalina* var. *lacustris* occur in Lochan an Daim.

Table 2. *List of zooplankton from the localities mentioned in text*

	Pitlochry Reservoirs	Lochan an Daim	Loch Kinardochy	Loch Moraig
CLADOCERA				
Diaphanosoma brachyurum (Liéven)	—	+	—	—
Daphnia hyalina var. *lacustris* Leydig	+	+	+	+
Simocephalus vetulus (O. F. Müller)	—	+	—	+
Ceriodaphnia reticulata (Jurine)	—	+	—	+
Bosmina obtusirostris Sars	+	+	+	+
Drepanothrix dentata (Eurén)	+	+	—	—
Eurycercus lamellatus (O. F. Müller)	—	+	—	+
Acroperus harpae Baird	+	+	—	+
Alona affinis (Leydig)	+	+	+	+
Rhynchotalona falcata (Sars)	—	+	+	+
Alonella excisa (Fischer)	—	+	—	+
A. nana (Baird.)	+	+	—	+
Peracantha truncata (O. F. Müller)	—	+	—	+
Chydorus sphaericus (O. F. Müller)	+	+	—	+
Polyphemus pediculus (Linneus)	+	+	—	+
COPEPODA				
Diaptomus gracilis Sars	+	—	+	—
Canthocamptus spp.	+	—	+	+
Cyclops (*Eucyclops*) *agilis* Koch, Sars	—	—	—	—
C. (*Paracyclops*) *affinis* Sars	—	—	+	—
C. (*Cyclops*) *strenuus* Fischer	+	—	+	+
C. (*Acanthocyclops*) *viridis* (Jurine)	—	—	—	+
Totals	11	21	8	16

The zooplankton of Loch Kinardochy consists of a *Diaptomus-Cyclops-Bosmina-Daphnia* complex in which copepods appear before Cladocera, though the latter remain later in the year. Figs. 6 and 7 show the changes in the abundance of the principal zooplankton species during the period covered by the present observations. It is of interest to compare the development of the *Daphnia* population in Kinardochy with that of Lochan an Daim (Fig. 7). It will be noted that although *Daphnia* was found in both lochs at approximately the same time, its first maximum was recorded in Loch Kinardochy on 16 June. In Lochan an

Daim, however, it did not occur until a month later, on 17 July, despite the apparent lack of competition from other species.

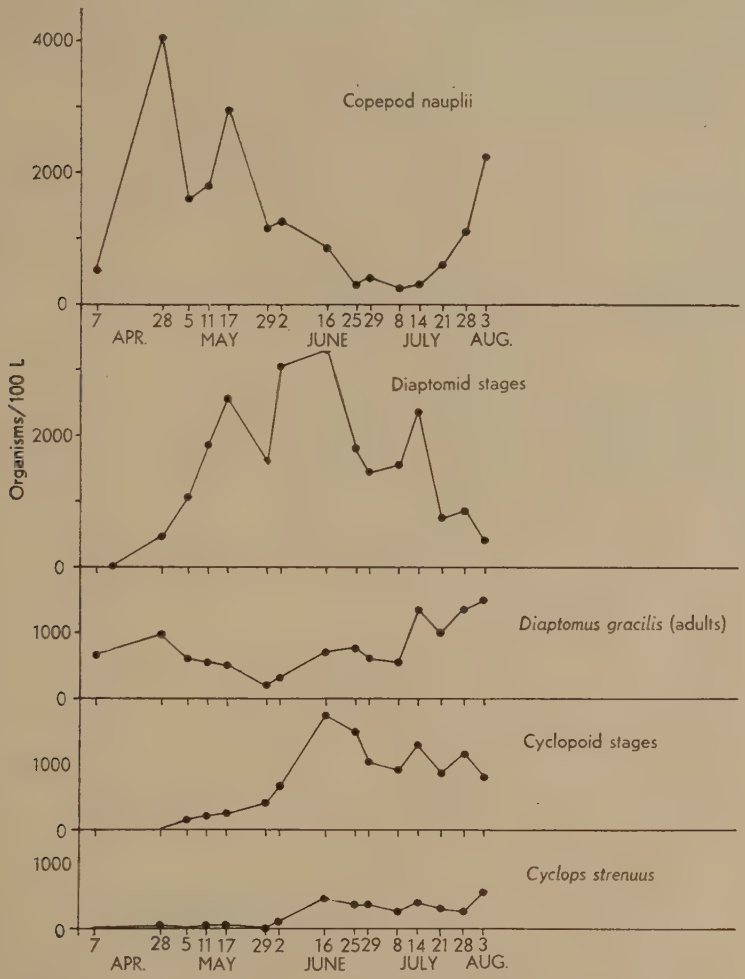

Fig. 6. The copepod zooplankton of Loch Kinardochy, 1954 (average of three sites).

Some consideration has been given, both in Loch Kinardochy and Lochan an Daim, to the effectiveness with which different species and age-groups of the same species can avoid being carried down the outflow (Table 3). It is apparent from this table that any losses which might be due to water replacement in Loch Kinardochy will be greatly reduced by the apparent rheotactic responses shown by these organisms in evading the draw down the outflow. It is clear that for each species success in evading the outflow increases with age, though it has been observed that adults in a senile condition do not show marked evasive responses.

Laboratory observations in an experimental trough have shown that, whereas Cladocera swim steadily and continuously against a current, copepods only begin to swim vigorously and erratically against a current when the latter accelerates rapidly as for example near the outflow. An attempt to determine the nature of

Table 3. *Effectiveness of avoidance of the outflow by zooplankton*

The figures show numbers present per 100 litres

	Average of all outflow samples (A)	Average of all samples from site near outflow (B)	Ratio B/A
Copepod nauplii	525	1330	2·5
Diaptomid stages	300	1286	4·3
Diaptomus gracilis	77	711	9·2
Cyclopid stages	145	590	4·0
Cyclops strenuus	14	167	11·9
Bosmina obtusirostris	128	1809	14·1
Daphnia hyalina var. *lacustris* — Loch Kinardochy	20	275	13·8
Daphnia hyalina var. *lacustris* — Lochan an Daim	90	80	0·9

this response suggests that it is not visual and it is believed that it is related to changes in hydrostatic pressure. The recent experimental observations of Knight-Jones & Qasim (1955) on responses of marine zooplankton organisms to changes in hydrostatic pressure add weight to this belief. The remarkable anomaly shown

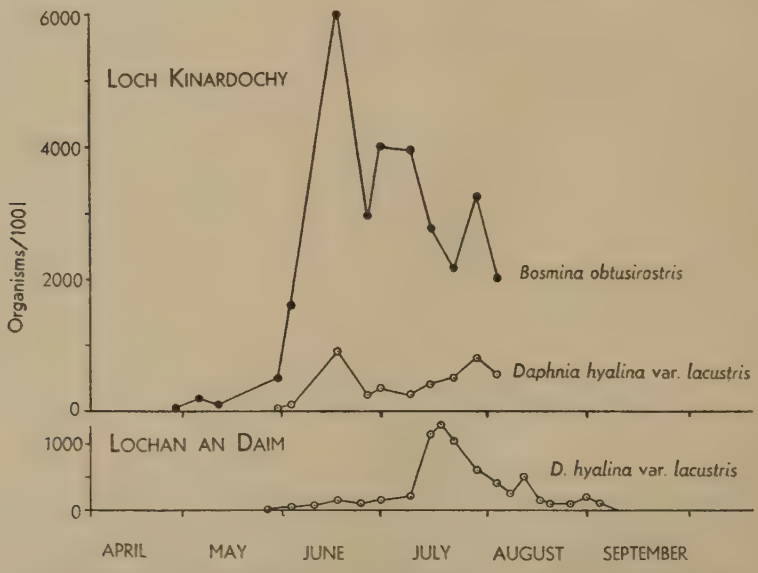

Fig. 7. Cladoceran zooplankton in Loch Kinardochy and Lochan an Daim, 1954.

by the figures in Table 3 for *Daphnia* in the two lochs may possibly be explained by the differences in their width and contour, there being a much greater chance of successfully evading a shallow, narrow outflow (as in Loch Kinardochy) than a broad deep one as at Lochan an Daim.

DISCUSSION

In the sea and in large lakes, the standing crop of plankton is usually taken as a measure of productivity. It has been tacitly accepted that a measure of the standing crop also gives an indication of the productivity of small lakes. The present results, however, seem to suggest that such estimates may be of little value and can even be very misleading. Detailed studies of communities other than the plankton and of the chemical characteristics of the four Scottish hill lochs already mentioned show strikingly how misleading such results can be. From a consideration of these biotic and chemical characteristics these lochs can be arranged in an ascending order of productivity as shown in Table 4. It will be noted from this table that, in terms of bottom fauna, Lochan an Daim is about three times as rich as Loch Kinardochy, in addition to being richer chemically. Comparisons of the

Table 4. *The productivity of four Scottish hill lochs in terms of submerged macrophytes, quantitative evaluation of the bottom fauna, chemical characteristics, and average zooplankton density*

	Loch Choin	Loch Kinardochy	Lochan an Daim	Loch Moraig
Replacement quotient	16	91	5	26
Indicator macrophytes	*Littorella*, *Lobelia*	*Littorella*, *Lobelia*	*Potamogeton natans*; some charophytes	*P. natans*; abundant charophytes
Bottom fauna per sq. ft { numbers	33	38	110	264
Bottom fauna per sq. ft { weight (g)	0·076	0·141	0·324	0·572
pH	6·14-7·52	6·80-7·67	7·22-8·08	7·38-8·13
Alkalinity (p.p.m. $CaCO_3$)	1·6-7·8	11·0-29·0	23.0-52·8	35·8-85·6
Free ammonia (p.p.m.)	0·168-0·756	0·103-0·636	0·974-1·240	0·095-1·290
Silica (p.p.m. SiO_2)	0·55-2·14	0·49-2·28	1·30-3·35	0·41-4·72
Zooplankton: average per visit (1950-52) per 100 l.	562	2790*	108	1211

* The 1952 figure for Loch Kinardochy. Figures for 1950 and 1951 are not included since they show the effects of treatment with rotenone in 1949-50 to eradicate pike.

phytoplankton and zooplankton estimates for these two lochs, however, show Loch Kinardochy to be very much richer than Lochan an Daim (Figs. 2, 3, 6, 7) and emphasize how erroneous productivity estimates based on the standing crop of plankton can be.

The above considerations would seem to suggest that quite erroneous estimates of the plankton productivity of lakes may be obtained if these are sampled without reference to the important physical factor of replacement. Moreover, the present results emphasize that, particularly in lakes with a low replacement quotient, sampling should be carried out at frequent intervals. It is also clear that, since changes in water level occur so rapidly (see Fig. 4), the full extent of replacement can only be assessed if continuous records of outflow are available. In view of this it is suggested that the productivity of such lakes can be best assessed by the study

and measurement of abundance of communities of plants and animals more stable than the plankton (e.g. bottom fauna, attached algal communities, etc.) which are not directly affected by the changes in the rate at which water is flowing through the loch.

It is of interest to note that Ruttner (1940) had drawn attention to the importance of the relationship between inflow and outflow in Alpine lakes. He states that it is this factor which brings about the spring and early summer population minima of almost all plankton species in such lakes despite their rate of reproduction being high during these periods owing to favourable environmental conditions. More recently Lund (1954, p. 172) has stressed the importance of winter floods in relation to the abundance and periodicity of the plankton diatom *Melosira italica* subsp. *subarctica* O. Müll. Their effects were particularly noticeable in Esthwaite Water and Blelham Tarn where the replacement time is relatively short. Decreases in the population of this diatom in these lakes, when growth is slow in winter, were on occasions found to be considerable.

Bearing in mind the effects of replacement, it is of interest to consider the increased plankton production which is sometimes observed in lakes where the water level has been raised. While such increases may have been in part due to decay in the inundated areas, it is clearly possible that the appearance of larger amounts of plankton could also be due to a reduction in replacement quotient due to the raising of the water level, although the volume of water passing through the lake has remained unchanged.

ACKNOWLEDGMENTS

The authors are indebted to Mr A. V. Holden and Mr N. C. Morgan for providing, respectively, the chemical data and quantitative information on the bottom fauna which appears in Table 4; also to Mr K. A. Pyefinch for helpful advice in the preparation of this paper.

SUMMARY

1. Four years' observations on the plankton populations of four Scottish hill lochs have shown that their density tends to be highest and that they are most stable in lochs with a low rate of water replacement.

2. Detailed studies were made during the spring and summer of 1954 on the plankton and replacement of water in one of these lochs having a low rate of replacement and in another with a high rate in order to determine more precisely the influence of this factor.

3. These studies indicated that at times the rate of replacement may be a factor of over-riding importance and may produce not only quantitative but also qualitative differences in the plankton.

4. Some observations have been made on the effectiveness with which different species and age-groups of individual species of zooplankton can avoid being carried down the outflows of lochs.

5. The results of this investigation indicate that the standing crop of plankton cannot be used as a measure of the productivity of small lakes, particularly where the replacement of water may be considerable.

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OBSERVATIONS ON THE BIOLOGY OF CHAOBORIDS AND CHIRONOMIDS IN LAKE VICTORIA AND ON THE FEEDING HABITS OF THE 'ELEPHANT-SNOUT FISH' (*MORMYRUS KANNUME* FORSK.)

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(With 6 Figures in the Text)

INTRODUCTION

During the course of work on the bottom fauna of Lake Victoria in relation to the feeding habits of fish, the opportunity was taken to make some observations on the biology of *Chaoborus*, the larvae of which, although relatively unimportant as fish food, are perhaps the most abundant mud-dwelling insects in the lake. Since practically no data are available on the effect of tropical lake conditions on the development of these insects, attention was paid mainly to the length of the life-cycle. In the mud with the *Chaoborus* were various species of chironomids, and of these, *Tanypus*, *Procladius* and *Chironomus* larvae were the most common. These larvae form an important part of the food of *Mormyrus kannume* Forsk. (the 'elephant-snout fish'), and it was necessary to know more about their biology. In the general features of their life-cycles they resemble *Chaoborus*, and for this reason they are being treated together. It is worthwhile also to discuss the relationship between the insect larvae and *Mormyrus kannume*, because a study of the food preferences of the fish throws some light on the biology of the insects, and, at the same time, features of the insect biology explain some apparent peculiarities of the fish diet.

It became clear during the work on the insects and from the fish food studies that certain events, such as the emergence of adults and the appearance of pupae in fish stomachs, occurred at regular monthly intervals. In order to explain this monthly periodicity the possibility of a lunar influence on the insects will be considered. Williams (1936) and Williams & Singh (1951) showed that some groups of terrestrial insects have periodicities of activity which are related to particular lunar phases but so far as is known there is no clear evidence of any correlation between the activity of aquatic insects and the moon. Hora (1927) suggested such a correlation with may-flies but his evidence was not very substantial.

MATERIAL AND METHODS

The larvae on which the paper is based were collected mainly from Ekunu Bay, a bay about twelve miles from Jinja on the northern coast of the lake (Fig. 1).

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This bay is fairly typical of many others, being partially bordered by papyrus swamp, gently sloping in cross section, and with a bottom of soft mud over much of its area. The bottom temperature usually lies between 25° and 26° C, seldom falling below 24° C. The dissolved oxygen content of the bottom water does not fall below 60% saturation and often stands about 80%.

A sampling station was selected near the centre of the bay where the depth is ten metres, and from there, samples of bottom mud were collected at approximately weekly intervals. In addition, other regions of the bay were sampled from time to time, and samples were taken from nearby Pilkington and Hannington Bays, from the Buvuma Channel and, less often, from other parts of the lake.

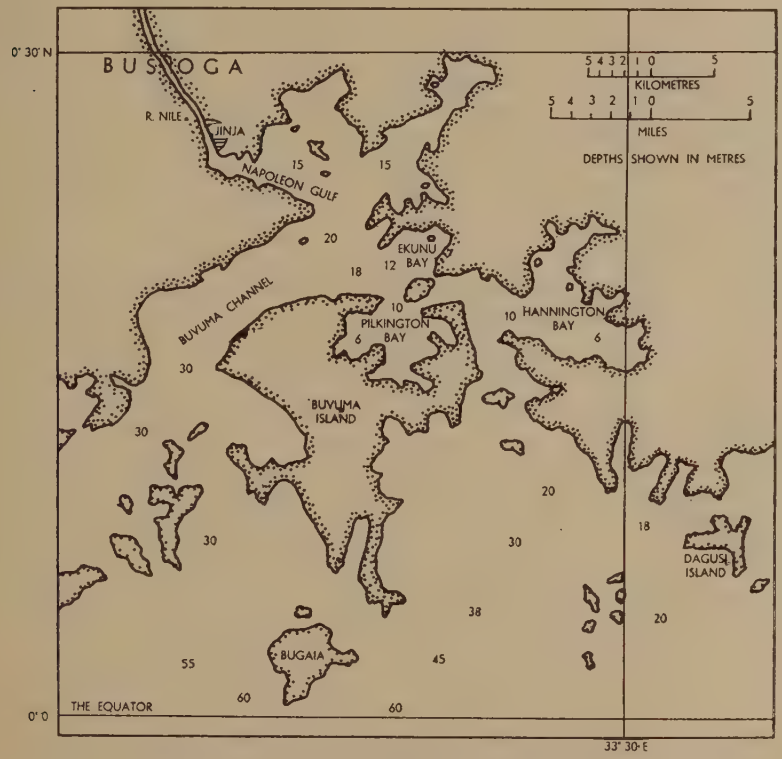

Fig. 1. Map of part of Lake Victoria showing Ekunu Bay and the other principal collecting regions around Jinja.

The bottom mud requires mention. In the bay it was very fine and flocculent, and there was not a well-marked mud-water interface. On examination it was found to be composed to a large extent of dead algae together with some living cells. In the main lake it was much more firm and compact, whilst in some deep water regions there was a sand or gravel substratum. It soon became evident that mud samplers such as the Birge-Ekman and the Friedinger grab were not collect-

ing a reliable sample in inshore waters. They sank too deeply into the mud before closing. A higher sampler such as the stratification sampler described and used by Lenz (1931) and Berg (1938) would probably have been suitable, but since there was not one available it was decided to use a Jenkin sampler, which collected a column of mud about 39 cm high and 40·7 cm^2 in area. This sampler was not designed for the study of the bottom fauna and the area covered is small. Berg (1938) discussing the efficiency of the Birge-Ekman pointed out that there was a large sampling error due to the variable horizontal distribution of larvae, and concluded that a double sample should always be taken to reduce this error. Using the much smaller Jenkin sampler correspondingly larger errors could be expected, but in the present work the faunal changes studied were qualitative rather than quantitative. In fact, four to eight samples were always taken in Ekunu Bay, and the quantitative results which are used are based on a large number of samples.

The mud was passed through a fine sieve of 60 meshes to 1 in. (approximately 23 meshes/cm), the larvae being sorted from the residue. Latterly, plankton hauls were also regularly taken, using a coarse net with a strangler closing mechanism in order to sample particular water layers. This method was employed only to determine when and where young *Chaoborus* larvae were present, no quantitative conclusions being drawn.

All the larvae collected, both chaoborids and chironomids, were measured, measurements of the total length and of the head capsule being taken by means of a calibrated eyepiece micrometer. Since the larvae often wriggled and turned, they were usually warmed on a glass slide to reduce their activity and facilitate measurement. From the head capsule measurements the larval instars were determined, and in the following account the larvae will be considered in relation to their instars. In the past, several workers have referred, especially with regard to *Chaoborus*, to 'one-third grown larvae', 'half-grown larvae', and so on, without any indication of which instars were involved except in the case of fully mature larvae. Only four instars are present in all Culicidae, and the available records make it seem likely that this is also the case in the Chironomidae. Here it is presumed that four larval instars are present in the latter group, and there is, accordingly, little difficulty in deciding to which instar a larva belongs on the basis of the head capsule measurements.

NOTES ON TAXONOMY

A major problem when dealing with a little-known group of insects in the tropics is the identification of species. Edwards (1930) briefly described the tropical species of *Chaoborus* as they were known to him from adult collections in the British Museum, but, useful as these notes are, there is little doubt that a number of species still awaits collection and description, whilst the larval and pupal stages of almost all tropical species are unknown. *Chaoborus* adults are usually difficult to distinguish, and the male hypopygia do not provide as good characters for identification as they do in other Culicidae, but the larvae are sometimes easier to separate.

The larvae in Lake Victoria could be separated into two groups with clear differences in the antennae and mouthparts. One of these proved to be *Chaoborus* (*Neochaoborus*) *anomalus* Edw., a species and subgenus created by Edwards for a collection of females from Entebbe, Uganda, and elsewhere. The adults are characterized by reduced antennae (only 8-10 flagellar segments are present), and by the interrupted vein M_2 in the wing. The collections studied by Edwards contained only females, and later (1932) he raised the question of whether parthenogenesis might occur in this species. Certainly males seem to be rare since several collections of the writer's are composed entirely of females. However, there is one male now in the British Museum recorded as coming from 'Nairobi 26.xi.34 in aeroplane'. Unfortunately the antennae are missing, but the wings show that vein M_2 is interrupted.

The identification of the other group of *Chaoborus* larvae has not yet been satisfactorily confirmed. Some reared adults belong to the subgenus *Sayomyia* but appear to be undescribed, so in the meantime the larvae have been designated *Chaoborus* species B. However, *C.* (*Sayomyia*) *pallidipes* Theo. is also known from the lake, and in fact is quite a common species. Since adults of *C. pallidipes* have been collected as they emerged from regions where larval species B occurs, it seems that these larvae may include two very similar forms one of which may be *pallidipes*. The larvae, pupae and adults are being re-examined as time permits and full descriptions will be published elsewhere.

The chironomid larvae could, on the whole, be satisfactorily identified to a genus, using European keys, although some groups of the subfamily Chironominae presented difficulty. Many of the African species are still undescribed so that it was fortunate that the common *Tanypus* and *Procladius* larvae proved, after rearing, to be *Tanypus guttatipennis* Goetgh. and *Procladius umbrosus* (Goetgh.) respectively. Both species are among those described and named by Goetghebuer (1935) from material sent to him from the Belgian Congo. For the identification of the chironomid adults I am indebted to Mr P. Freeman of the British Museum.

THE BIOLOGY OF *CHAOBORUS*

Chaoborus larvae are probably the most common insect larvae in the lake and their total numbers must be very considerable. In Ekuna Bay the average density was 2000-2500 larvae per sq. m. In addition, there were nearly 1000 chironomid larvae; hence *Chaoborus* comprised about 70% of the total insect fauna. In the bay 60-70% of the chaoborid larvae were *C. anomalus*, i.e. about 1500 per sq. m. This species is most abundant at moderate depths between 5 m and 15 m; in deeper water it was not uncommon at 30 m, but it was absent from samples taken at 60 m. At a station in the Buvuma Channel, where the depth was 20 m, and at deeper stations *Chaoborus* species B was dominant with a density of about 1400 larvae per sq. m. The numbers collected in Buvuma Channel were very variable, and the density quoted is based on some 150 samples taken from there at different times. In Pilkington and Hannington Bays *C. anomalus* was most com-

mon. In Ekunu Bay, where regular observations were made, the life-cycles of *C. anomalus* and *C.* species B were similar, so they may be discussed together. For convenience the life-cycle can be considered as having four stages: the egg stage which is short; the planktonic stage which is composed of the first and second instars; the mud-dwelling stage comprising the third and fourth instars and pupa; and the flying stage.

(*a*) *The egg stage*

Eggs of *Chaoborus* were not collected in the field, but a number of females of *C. pallidipes* which were captured near the laboratory laid eggs in a dish of water. All the eggs sank to the bottom of the dish, and although a piece of plant material had been left semi-submerged, there were no eggs attached to it. Some eggs were clumped together but a number of others lay free. Each was sausage-shaped and surrounded by a thick layer of jelly-like substance. The measurements were 0·47 mm in length and 0·11 mm in width. Two days after they were laid a few larvae had hatched and several more could be seen wriggling within the egg capsule (temperature 20-24° C). Many were at the 'eyed' stage. By the following day many more had hatched, and on the fourth and fifth days the remainder were free, but some eggs showed no signs of development and died. When the larvae hatched out they measured about 1 mm and there was a noticeable quantity of yolk in the gut. Unfortunately all died in the first and second stadia. It is probable that under natural conditions the egg stage lasts two to four days and that the other species are similar in this respect.

(*b*) *The planktonic stage*

All the first and second instar larvae of *C. anomalus* and *C.* species B were planktonic, with the exception of a few second instars which were found in the mud. Berg (1937), working with *C. flavicans* (Meig.) in Esrom Lake, found that the eggs were laid near the shore and that the young larvae hatched out there. Thus there was a high density of young planktonic larvae inshore, and after a time these larvae moved gradually into deeper water still leading a planktonic life. Later, they entered the mud. It is not clear which instars are involved, but it seems not unlikely that he was dealing with first and second instar larvae until the mud-dwelling stage was reached. Lindquist and Deonier (1943) also noted a high density inshore of the young larvae of *C. astictopus* D. & S. in Clear Lake. These also moved outwards as they increased in size.

The situation was different in Lake Victoria. There was no inshore aggregation of larvae, and plankton hauls showed that first and second instars of *C. anomalus* and *C.* species B could be found in Ekunu Bay far from the shore, including very recently hatched larvae with yolk still present in the gut. Juday (1921) found that eggs of *C. punctipennis* Say. were laid on the surface of Lake Mendota and that they sank to the bottom mud where they hatched. It seems likely that egg-laying may be similar on Lake Victoria since at a deep-water station, five miles from land (depth 57 m), first and second instars were collected. In this latter collection the

larvae were mainly *C.* species B with a few *C. anomalus*. It is noteworthy that less than 1% of the larvae were collected from the 10-0 m stratum, whilst in Ekunu Bay, where the total depth is only about 10 m, very few larvae were collected from the 2-0 m stratum. This difference may be correlated with the difference in light penetration in the bay, which is relatively rich in plankton, and in the open lake, where the plankton is more sparse and light penetration is greater.

When plankton hauls were taken at this deep-water station a thermocline existed between 35 and 38 m; below the thermocline larvae were present although there was less oxygen than in the epilimnion. Third and fourth instars of both *C. anomalus* and *C.* species B have been collected from the mud in the Buvuma Channel at times when the bottom water was deoxygenated, so the larvae at all stages are tolerant of low oxygen conditions. Juday (1908) included *C. punctipennis* among the insects which can live under anaerobic conditions, and later (1922) found young larvae of this species in Lake Mendota inhabiting the hypolimnion by day in the absence of oxygen until they were one-third to one-half grown. Miller (1941) also noted the occurrence of this species uniformly distributed below the thermocline.

Worthington & Ricardo (1936), sampling several East African lakes to determine the movements of plankton, found on Lakes Edward and Bunyoni that by day the *Chaoborus* larvae were vertically distributed roughly according to size, the smaller larvae being near the surface, and the larger, 8-9 mm in length, deeper down. This was most marked in Lake Edward where they took samples to 55 m. (Below 50 m there was practically no oxygen but a trace of hydrogen sulphide.) Their results suggest that in these lakes the third and fourth instar larvae

Table 1. *Life cycle of* Chaoborus *species*

Stage		Egg	I	II	III	IV	Pupa
Approximate duration (days)		2-4	4-6	6-10	12-16	25-30	2-3
Observed total lengths (mm)	*C. anomalus*		1·24-1·95	2·02-3·43	3·27-5·30	4·68-7·64	
	C. species B		1·32-2·34	2·10-3·74	3·12-6·70	5·30-8·81	
Observed head capsule lengths (mm)	*C. anomalus*		0·187	0·312	0·530	0·889	
	C. species B		0·234	0·390	0·655	1·092	

might be included in the planktonic stage, since larvae of 8 or 9 mm are very unlikely to be second instars. At night the larvae were concentrated near the surface. Unfortunately, it was not possible to reinvestigate these lakes. Juday (1921) also observed a slight degree of relationship between the size of planktonic larvae and the depth at which they were found. In Lake Victoria, however, regular samples were not taken at a deep-water station, and the few which were taken showed uniform distribution of the larvae. In Ekunu Bay there were no marked differences in the size of larvae that could be related to depth.

Table 1 shows the range of sizes observed in the first and second instars of *C. anomalus* and *C.* species B, and the duration of each stadium. The species were similar in having a planktonic stage lasting about two weeks.

(*c*) *The mud-dwelling stage*

As a general rule the larvae change their mode of life when they reach the third instar, living in the mud by day, and returning to the plankton only at night for feeding. Beyond confirming these nightly migrations both in field and laboratory conditions no investigation was made on this subject.

The mud-dwelling stage is the longest in the life-cycle, lasting nearly six weeks and comprising the third and fourth instars and the pupa. Table 1 shows that the whole cycle from egg to adult lasts about two months; it is of interest therefore to note that Frankenberg (1915) (see Berg, 1937, p. 26) found that under optimum conditions in aquaria the development of *Chaoborus flavicans* was two months. Muttkowski (1918) found the larval life of *C. punctipennis* in Lake Mendota lasted six to seven weeks in the summer, and Miller (1941), working with the same species, records adults emerging mainly during late June and early July, and adults of the next generation at the end of August and early September. That is to say, the life-cycle of the summer generation of *C. punctipennis* lasts about two months. This suggests that a life-cycle of two months may be a general feature of the biology of

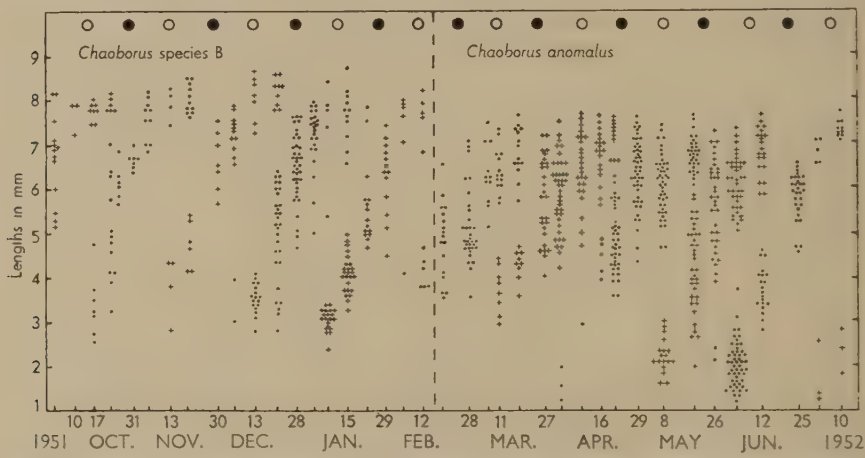

Fig. 2. Growth of *Chaoborus* species B (October-February) and *Chaoborus anomalus* larvae (February-July) in Ekunu Bay. The total lengths of all larvae collected in four mud samples have been plotted. From April onwards planktonic larvae are included. Two populations of each species are present, and these are illustrated by the use of crosses for one population and dots for the other.
● = New Moon ○ = Full Moon

species of *Chaoborus* living under warm summer conditions in temperate climates or under tropical conditions. However, shorter development times may be possible for some species. For example Deonier (1943), in laboratory experiments with *C. astictopus*, found that the whole life-cycle could be completed in less than a month, although it cannot be deduced that this is the case in nature.

From regular measurements of the larvae the growth-rate was determined, and this is illustrated in Fig. 2 which will be discussed later. Growth is steady until late in the fourth instar, i.e. when *C. anomalus* larvae are more than 6 mm and

C. species B more than 7 mm long. At this point the growth curve begins to level out, the larvae adding little to their length. There is, however, an increase in bulk in the larvae, due to the accumulation of food reserves prior to pupation, not shown by the figure.

Dyar's rule, that changes in the head capsule measurements of successive instars follow a geometrical progression, was found to obtain in the case of *Chaoborus*. A ratio of increase ('*r*') of approximately 1·68 applied to the head capsules of both *C. anomalus* and *C.* species B. A straight line graph is obtained when the logarithms of the head lengths are plotted against the number of the instars.

OBSERVATIONS ON *TANYPUS GUTTATIPENNIS* AND *PROCLADIUS UMBROSUS*

In Ekunu Bay *Tanypus guttatipennis* and *Procladius umbrosus* were amongst the most common chironomids. They were rather similar to *Chaoborus anomalus* in distribution, being sometimes collected from deep water but in small numbers. Associated with them in the mud in Ekunu Bay were *Chironomus* larvae of the *plumosus* type, an occasional member of the Chironomariae connectentes group, one or two *Tanytarsus* species (*heusdensis-gregarius* group) and *Clinotanypus* sp. With the exception of *Chironomus*, these were all present in small numbers and were of little importance as fish food. In shallow water, on sand and gravel and amongst weed, there was a greater variety of species, principally Tanypodinae and Chironominae. It is noteworthy that Orthocladiinae were rare. In temperate waters this group is always well represented both in numbers and species, but it appears that they have not colonized warmer waters to the same extent. Temperature is probably the limiting factor since collections made in the cold streams of the Kenya Highlands contained a large proportion of typical stream-dwelling genera such as are found in Europe, e.g. *Trichocladius*, *Euorthocladius* and *Eukiefferiella*. The results of the German Sunda Expedition point to a similar conclusion, that Orthocladiinae are not so dominant in warm as in cold water. The only orthoclad in the collections from Lake Victoria was an inshore living larva rather similar to that of *Microcricotopus*.

As in the case of *Chaoborus*, all *Tanypus* and *Procladius* larvae were measured. It became evident that only two instars, the third and fourth, were present at the sampling station near the centre of the bay. Very occasionally a late second instar larva was taken, but the usual habitat of the first and second instars was not determined. The mesh of the sieve was fine enough to preclude any likelihood of their being lost during sieving. Although several bottom samples were taken inshore in Ekunu Bay, no real search was made, since attention was being concentrated on those stages which were important as fish food. The probability is that the eggs are laid inshore and that they hatch there, the larvae migrating outwards about the time when they become third instar larvae. Larval migrations to and from the shore are not uncommon amongst aquatic insects, e.g. Berg (1938) demonstrated migrations of *Tanypus* larvae from the 2-4 m zone to the 10-12 m zone in Esrom Lake in less than a month. However, there is little known about

how the larvae are stimulated to migrate, how they travel, how they are orientated and so on.

It has often been recorded that the larvae of the sub-family Tanypodinae are carnivorous, but this is not true for all species; in fact, probably few species are obligative carnivores. Whilst larvae of *Clinotanypus* not infrequently contained the remains of small larvae such as *Tanytarsus*, no insect remains were ever found in the guts of *Tanypus guttatipennis* or *Procladius umbrosus*. The former fed entirely on algae such as *Melosira*, *Pediastrum* and *Staurastrum*, whilst the latter almost always had several Ostracods as well as algae in the stomach. Both would appear to feed on or near the surface of the mud and to be more selective than the larvae of *Chironomus* which feed as they burrow under the mud.

The life-cycle of both species lasts two months, and although the early instars were not collected, it is thought that the general time sequence of the stadia is similar to that of the *Chaoborus* species. The third stadium lasts about two weeks, and the fourth, three to four weeks. Fig. 3, which will be discussed later, shows the growth-rate of the third and fourth instars of *Tanypus guttatipennis*. The measurements of *Procladius umbrosus* fit a similar pattern. As in the case of *Chaoborus*, there is a levelling of the growth curve when the larvae are fourth instars due to their growing stouter rather than longer.

Dyar's ratio was calculated for both species from the head capsule measurements of the third and fourth instars alone. In the case of *Tanypus guttatipennis*, '*r*' = 1·5; in that of *Procladius umbrosus*, '*r*' = 1·63. Using these ratios the head capsule lengths in mm of all instars should be:

	I	II	III	IV
Tanypus guttatipennis	0·164	0·249	0·374	0·561
Procladius umbrosus	0·157	0·257	0·421	0·686

A few second instar larvae of *Tanypus guttatipennis* which were collected had, in fact, head measurements identical with those estimated. Straight line graphs are obtained when the logarithms of these figures are plotted against the instars.

POPULATIONS AND PERIODICITIES

Under the generally uniform conditions which are found in a tropical lake it might be expected that there would be more or less continuous emerging, mating and egg-laying, with a resultant mixed population of larvae of all stages. That this is not the case is evident from Figs. 2 and 3, which show that the larvae are found in well-marked groups of approximately the same size. Furthermore, it can be deduced from the relatively sharp disappearance of mature larvae from the mud that they pupate and emerge together. This applies to both *Tanypus guttatipennis* and *Procladius umbrosus*, and to the two species of *Chaoborus*. Also clear from the figures is the presence of two separate size-groups of larvae of each species. When one group is nearing maturity, there is another about half-grown co-existent in the mud. These groups are separate populations of each species.

This feature is unexpected, but more so is the fact that they are separated in time by one lunar month. To illustrate this, the times of appearance of the new and full moons are shown in the figures.

In the case of *Chaoborus*, it appears that when one population is in the late fourth instar, the other is leaving its planktonic life and entering the mud as young third instar larvae. As Fig. 2 shows, the latter larvae grow quickly, whilst the growth-curve of the first population is levelling out. In the *C. anomalus* curve it seems that the two populations mix, but although the older population is not adding much to its average length, the larvae are becoming stouter and are accumulating food reserves for pupation. The younger population is probably physiologically unready for pupation. The apparent mixing of populations is also more marked in the case of *C. anomalus* because the larvae only grow to about 7·5 mm in length, whilst the populations of *C.* species B are better defined partly because these larvae grow to about 8·5 mm.

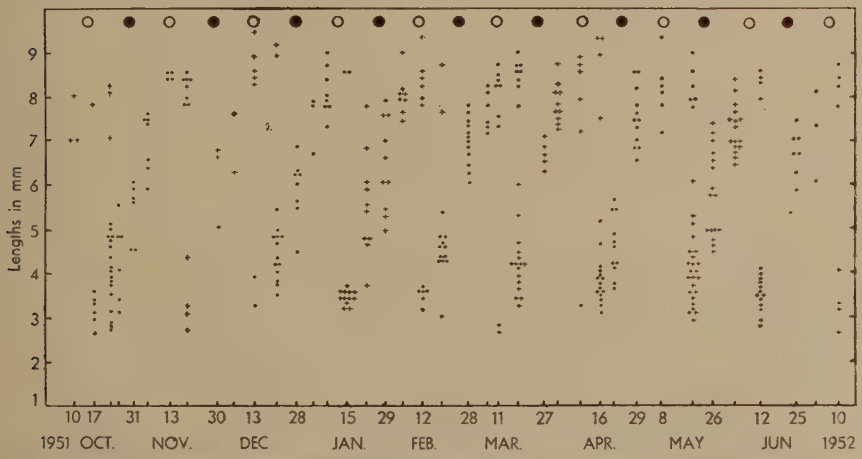

Fig. 3. Growth of *Tanypus guttatipennis* larvae in Ekunu Bay. The total lengths of all larvae collected in four mud samples have been plotted. Two populations of the species are present, and these are illustrated by the use of crosses for one population and dots for the other.
● = New Moon ○ = Full Moon

When the first and older population emerges, the second has reached the fourth instar, and by the time this latter population is ready to pupate, i.e. after another month, the first has emerged, eggs have been laid, and the young larvae have passed through the planktonic stage and entered the mud-dwelling stage. The relative positions are thus reversed each month. Since the life-cycle lasts two months and the populations are separated in time by one month, the end result is an alternation of populations with emergences at monthly intervals.

An almost similar sequence of events occurs in the case of *Tanypus guttatipennis* and *Procladius umbrosus*. The main difference probably lies in the different behaviour of the first and second instars, which were not collected. What is

interesting is the relatively sudden appearance of the third instars in the centre of the bay. Fig. 3 illustrates this point for *Tanypus guttatipennis*, and the regularity of their appearance is accentuated in Fig. 6 which shows the numbers of larvae collected from the mud. The monthly peaks represent the times when the third instars appear at the sampling station. These influxes are perhaps analogous to the entry of third instar *Chaoborus* into the mud.

It is not yet known whether this feature of populations separated in time is characteristic of other species in the lake. *Chironomus* larvae were collected and measured regularly to try to detect a similar growth pattern, but the larvae could not be separated into distinguishable size-groups. There was always a very large scatter when the lengths were plotted, despite the fact that the larvae grew to 14 or 15 mm in length. However, although size-groups could not be separated, there is good reason to believe that physiologically well-marked populations

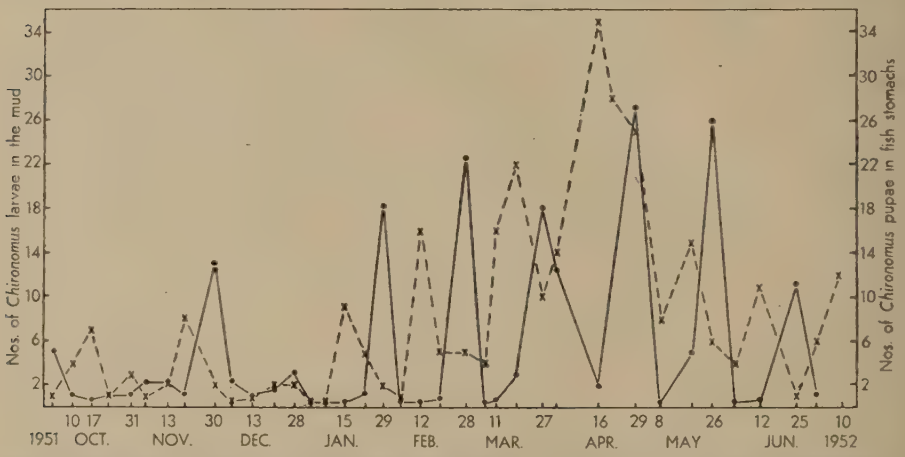
Nos. of Chironomus larvae in the mud
Nos. of Chironomus pupae in fish stomachs
34
30
26
22
18
14
10
6
2
10 17 31 13 30 13 28 15 29 12 28 11 27 16 29 8 26 12 25 10
1951 OCT. NOV. DEC. JAN. FEB. MAR. APR. MAY JUN. 1952

Fig. 4. Fluctuations in the numbers of *Chironomus* larvae in the mud (x- - -x), and in the numbers of *Chironomus* pupae in the stomachs of *Mormyrus kannume* (●———●), in Ekunu Bay. The numbers of larvae are those collected in four mud samples; the numbers of pupae are the average numbers per 100 larvae of all species.

existed. Records of the number of pupae in the stomach contents of *Mormyrus kannume* showed that at regular monthly intervals large numbers occurred, whilst at other times they were absent or present only in small numbers (Fig. 4). Since there were always larvae in the mud, it may be deduced that there were separate populations and that the life-cycle is a multiple of one month. In addition, in the graph showing the numbers of *Chironomus* larvae in the mud (Fig. 4) there are monthly peaks which coincide with those of *Tanypus guttatipennis* (Fig. 6). This suggests that the life-cycles may be similar, and that the early larval stages of *Chironomus* live inshore and move outwards when they are older.

Since the life-cycles of these common species can be related to units of one month, the possibility of a lunar periodicity arises. In Figs. 2 and 3 the new and full moons are shown in relation to the larval stages, and it is evident that the

larvae of both populations of each species pupate at the same lunar phase, just before new moon. It is of course inevitable, given a two month life-cycle and two populations separated by one month, that emergences could be correlated with a particular phase of the moon. However, it is noteworthy that the sequence of events should be so regular, and that the emerging times of both *Chaoborus* species, *Tanypus guttatipennis*, *Procladius umbrosus* and the *Chironomus* species should coincide. Further evidence pertaining to this point was obtained when pupal skins were found on the water surface. On one occasion when a pupal sweep was made in Ekunu Bay after a recent emergence, it was found that the skins represented at least ten species. As would be expected from the larval densities, the two species of *Chaoborus* were dominant, but the skins of *Tanypus guttatipennis*, *Procladius umbrosus*, *Chironomus* sp., *Tanytarsus* spp., *Cladotanytarsus* sp. and *Ablabesmyia* of the *monilis* group were also present. Samples of adults from large swarms in other parts of the lake also suggested that emergences were synchronized, and that a number of species emerged together, although as a rule one or two were dominant.

Although the larvae of each population comprise a natural group, there is an appreciable scatter between the smallest and the largest larvae. Since the adults emerge together, it seems likely that there is some form of diapause, probably late in the fourth instar or in the pupal stage, which results in the synchronized emergence. Although it is not uncommon to find the adults of freshwater insects emerging together, there is as yet no explanation of the mechanisms involved in this phenomenon.

No regular observations were made on any other East African lake, but some bottom samples were taken during a short visit to Lake George and the Kazinga Channel. The larvae of *Chaoborus ?anomalus*, *Tanypus ?guttatipennis* and *Procladius ?umbrosus* were the most common forms; they were very similar to the larvae in Lake Victoria. *Chaoborus* species B larvae were not collected, either because too few samples were taken or because it was absent, Lake George and the Kazinga Channel being only 3 m or less in depth. However, the fact emerged that two size-groups or populations of each species could be distinguished, which suggests that there was a cycle of alternating populations similar to that in Lake Victoria.

THE ADULT SWARMS

Swarms of 'lake-flies' on Lake Victoria, and on other African lakes, are well known to people living near the lake shores. The swarms may extend several hundreds of feet high, but no very accurate estimate of their dimensions has been made. Suffice to say that they can be seen from a distance of several miles, often as a tall black column. No observations have been made on the swarming process, and since swarming may take place many miles from land it is difficult to envisage a focal point over which the swarm aggregates. It may be that the swarms are formed and held together by sound emissions from the flies. The latter can certainly perceive notes of certain frequencies. The swarms are subject to the

prevailing winds as a result of which they are often swept ashore where they may constitute a serious nuisance in townships.

Since casual observers were of the opinion that swarms of flies occurred at definite phases of the moon, particularly around new moon, it seemed advisable to keep a record of the times of occurrence of swarms. Unfortunately, Jinja, situated at the head of Napoleon Gulf, was protected by land from the main lake, and typical 'lake-fly' swarms were neither seen nor experienced there. However, a number of voluntary observers in Entebbe and on Dagusi Island kindly kept a record of the times they saw swarms. Most of the recording was done in the period December 1950 to September 1951, but there are numerous though less complete records after this period until July 1952. The results have therefore been recorded in the manner shown in Fig. 5. Each swarm has been plotted in relation

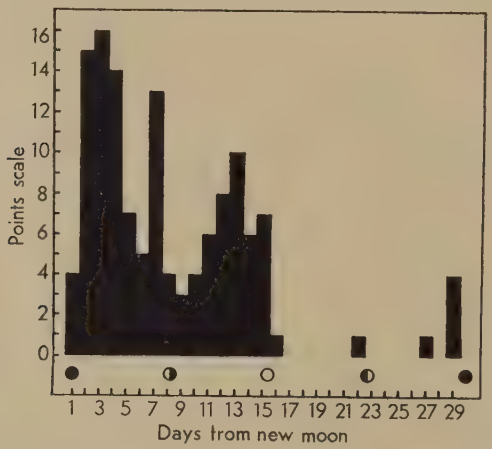

Fig. 5. Combined records of 'lake-fly' emergences from Lake Victoria (December 1950-July 1952) in relation to the lunar cycle. The ordinate scale is arbitrary, points being accorded on the basis of the size and number of swarms (see text). ● = New Moon; ○ = Full Moon

to the new and full moon of the month in which it occurred, and the figure gives a composite picture of all the records. It proved difficult to get an exact estimate of the number and size of swarms, so an arbitrary system has been adopted of according to a small or medium sized swarm, as estimated by the observer, one point; to a large swarm, or two or three small swarms, two points; and to many swarms, and records of widespread emergences, three points. On this basis it is likely that an emergence from such a bay as Ekunu would merit one point at most. The records almost all fall in the period when the moon is waxing, i.e. between new and full moon, and there is a well-marked period, when the moon is waning, when very little swarming was seen; the two records after full moon were in fact individual small swarms. The peak of emergences occurs about two days after new moon, and there is a suggestion of another peak three or four days before full moon. It would be desirable to have many more records, but the present ones

strongly suggest that there is a significant correlation between emergences and the new to full moon period.

A few samples of flies from swarms were obtained, but not enough to yield much information. It may be said that only *Chaoborus* and chironomids were encountered, and that the samples were usually composed of several species, one or two often outnumbering all the others. More information is required on the species composition of the swarms, and on the areas from which they originate. The Ekunu Bay flies emerge about the time of the new moon, but it is not clear whether this is characteristic of the species occurring there, or whether it is a function of the habitat or region. An emergence mentioned earlier, when pupal skins were collected, occurred on or just before 26 May, three days after new moon, but nearby in the Buvuma Channel a small number of *Chaoborus* emerged on 19 May, three days before the new moon. Possibly there is an indirect lunar influence, but as yet there is no other regularly varying factor known which might afford an explanation.

It has been presumed from the general distribution of the recorded swarms and from the species collected that they originate principally, if not entirely, from larvae living in the sublittoral and profundal zones. There is, however, a great variety of species, quite abundant in numbers, in the littoral zone, and these should perhaps be considered separately. Less than two months' regular observations were made on these inshore species, and, at the time, the work was unconnected with the question of periodicities. Three funnel traps, each covering 0·25 sq. m, were used to capture emerging adults. The traps were set over different types of substrata of different depths, the deepest being 5 m, and the catch was removed each morning. During six weeks there was seldom a day on which no adults emerged into each trap, but the numbers fluctuated considerably. The trapping period was too short to draw definite conclusions on the times of emergence, but the numbers caught increased in the week before new moon, the peak being reached a day or two after new moon. However, statistically, the differences in the catches at each lunar phase were not significant, and a longer series of results is required to determine whether there is a lunar influence on the inshore species.

THE FEEDING HABITS OF *MORMYRUS KANNUME*

Mormyrus kannume is sometimes called the 'elephant-snout fish' because of its long snout or rostrum. The fish is widely distributed in East African lakes and in the Nile system, but little is known of its habits, or of its eggs and young. It probably has an annual breeding cycle (East African Fisheries Research Organization 1952). It is a bottom living fish feeding principally on the early stages of insects, such as the larvae of Chironomidae and Trichoptera, and the nymphs of Odonata and Ephemeroptera; prawns are sometimes an important food item. Graham (1929) and Worthington (1929) made a few observations on the stomach contents, and in general it may be said that the food is a reflection of the bottom fauna of the region in which the fish is living and feeding.

During the period when bottom samples were being taken in Ekunu Bay, *M. kannume* were being gill-netted at weekly intervals as part of the programme of the East African Fisheries Research Organization. Hence, fish which had been caught within a few hours of the bottom samples being collected were available for examination. In Ekunu Bay the food of the fish was mainly composed of three species of larvae—*Tanypus guttatipennis*, *Procladius umbrosus* and *Chironomus* larvae of the *plumosus* type; *Chaoborus*, *Clinotanypus*, *Tanytarsus* and a few other genera were represented in unimportant quantities.

There is no standard method for the assessment of the food of fish. The method used depends to a large extent on the feeding habits of the fish, the degree of accuracy required, and on personal preference. Hynes (1950) gives a good account of the various methods that have been used and their merits. In the case of *Mormyrus kannume* it was found convenient to examine only a fraction of the total

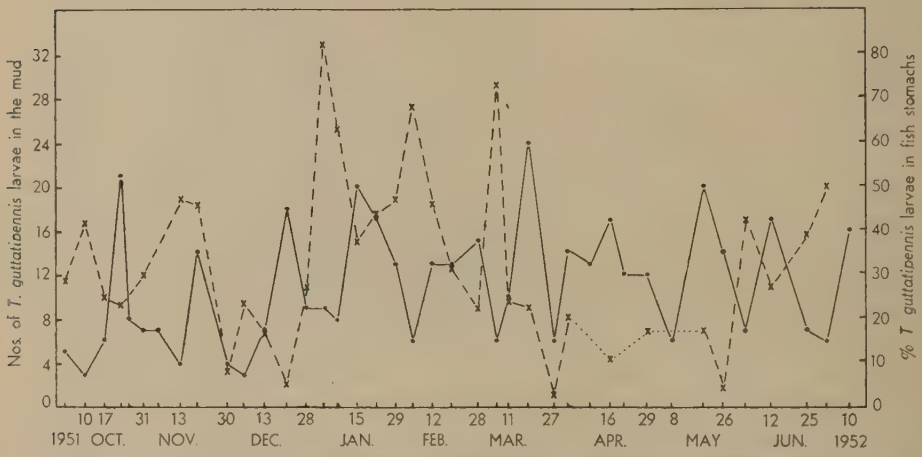

Fig. 6. Graphs showing the regular fluctuations in the numbers of *Tanypus guttatipennis* in the mud (●———●), and in the percentages of the same species in the stomachs of *Mormyrus kannume* (×- - -×), in Ekunu Bay. The numbers of larvae are those collected in four mud samples; the percentages are based on the examination of from four to eight fish stomachs.

stomach contents since one stomach might contain the remains of several thousand larvae. The contents were mixed with water and a random sample was removed with a pipette. Since the head capsules could be easily identified, each was regarded as representative of one larva, although often the head was detached from the rest of the body. Between four and eight stomachs were examined each week, one hundred larvae being identified from each stomach. The average number of larvae of each species present in the samples was then converted to a percentage for the stomach contents as a whole. A note was also taken of the number and species of pupae in the samples. In addition, an estimate was made of the total stomach contents, numbers from 0 to 5 being used to express the range from empty to very full stomachs.

The noticeable feature of the results is the regular variation in the percentages of *Tanypus* larvae in the stomachs (Fig. 6). These larvae were the principal food items at monthly intervals, as shown by the peaks. In the same figure are the numbers of *Tanypus* collected from the mud each week, and it is surprising to find that when the larvae are most abundant in the mud, i.e. when both populations are together, they are usually least common in the stomachs. The large numbers in the stomachs coincide with the times when the larvae in the mud have reached the fourth instar but are not yet near pupation, and before the third instars of the second population have appeared in the mud at the sampling station. It might have been expected that the reverse would take place, namely, that the fish would feed to an even greater extent on *Tanypus* when the second population entered the feeding grounds. However, the explanation lies in the preference of the fish for *Chironomus* larvae which replace *Tanypus* in the stomachs as the principal food. Fig. 4 shows that the numbers of *Chironomus* in the mud fluctuate and that peaks occur at regular monthly intervals. In fact, the peaks of abundance of *Chironomus* and *Tanypus* coincide. It is at these times that *Mormyrus kannume* feeds mainly on *Chironomus*. After the adults emerge there are fewer *Chironomus* in the mud, and the fish revert to feeding mainly on *Tanypus*, although the number of these have also decreased due to emergences. Thus, throughout each month the fish diet changes, first *Tanypus*, then *Chironomus* being the principal food. At the same time the larvae of *Procladius* form a significant part of the food, but possible regular fluctuations are masked by the *Tanypus-Chironomus* cycle.

The main point which concerns the fish is that owing to the presence of two populations of larvae separated in time, there is a constant and abundant food supply, no doubt in excess of requirements, in Ekunu Bay. Since a number of species pupate and emerge about the same time, there would be a period when there were few or no larvae in the mud were it not for the fact that a second population replaces that which emerges. As a result of this, estimates of the total stomach contents showed no regular variations, the stomachs being usually half-full to full. There was a suggestion in the figures that the stomachs were rather more full at the times when *Chironomus* was the principal food, but this was not very marked.

Mention may be made at this point of the relationship between *Chaoborus* larvae and *Mormyrus*. Although they were the most common larvae in the mud, fish stomachs contained very few. The probable explanation lies in the habit these larvae have of making vertical migrations at night from the mud into the open water, and in the fact that *M. kannume* feeds at night, thus missing a valuable food supply. Although stomachs contained small numbers of *Chaoborus*, it was noticeable that *C.* species B larvae were more commonly present than *C. anomalus*. This is a reversal of their relative abundance in the mud, and suggests a difference in the habits of the two species which might be clarified by a study of their nocturnal habits.

In fish food studies, use is sometimes made of the 'availability factor' or 'forage ratio' to express the relationship between the abundance of each food item in the

fish stomach and its abundance in the feeding ground. In practice it would be of value since a factor for each type of larva could be estimated, and the factors obtained could then be compared with 'availability factors' of larvae in other regions. The availability of particular food organisms to different fish could also be compared. In Ekunu Bay, for example, *Chaoborus* would have a very low factor, being abundant in the mud yet uncommon in the stomachs. More particularly, *C. anomalus* would have a lower factor than *C.* species B for reasons already mentioned, suggesting a difference in the biology of the two species. However, a difficulty becomes apparent when the larvae of *Tanypus guttatipennis* are considered. A factor estimated at any time becomes invalid a week or two later. The larvae are abundant in the fish stomachs before they reach their peak in the mud, whilst later, when the numbers in the mud have increased, the fish feed on them to a lesser extent—an anomaly which has been explained earlier. This example is not necessarily unusual; such complications may be common when the food organisms are insects which might emerge during the period work is in progress. It serves, however, to emphasize the difficulty of estimating a reliable 'availability factor', and the necessity in fish food studies of studying not only the fish, but the biology of the food organisms themselves, before the relationships between the fish and its food can be clearly understood.

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SUMMARY

1. The life-cycles of *Chaoborus anomalus* and an undetermined species of *Chaoborus* were studied in Ekunu Bay, Lake Victoria, and were found to last two months. The larval life comprised four instars of which the first two were planktonic, and the third and fourth were mud-dwelling by day and planktonic by night.

2. *Tanypus guttatipennis* and *Procladius umbrosus* also had life-cycles lasting two months. The early stages were not collected from the centre of the bay where the third and fourth instars lived.

3. In Ekunu Bay there were two populations of each of these species separated in time by one month. As a result, emergences occurred at regular monthly intervals.

4. The length of life-cycle of *Chironomus* sp. (larvae of the *plumosus* type) was not determined, but it was established that it was possibly two months, and certainly a multiple of one month.

5. Since these five species, and a number of others, emerged regularly about the time of the new moon, it is suggested that there may be a lunar influence on their biology.

6. Large 'lake-fly' swarms were recorded from different regions of the lake. Almost all the swarms occurred during the period when the moon was waxing; the peak of emergences was 2-3 days after new moon.

7. The stomach contents of *Mormyrus kannume* were studied, and regular fluctuations in the species of larvae which formed the principal food were correlated with fluctuations of the same species in the mud.

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* Quoted at second hand.

MOVEMENTS OF SOME BRITISH SMALL MAMMALS

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(With 9 Figures in the Text)

During the course of 'mark and release' live trapping for the estimation of the population of small mammals (Brown 1954), data was accumulated with respect to the animal's daily movements. Whether one is entitled to regard any of these records as illustrating true home range is open to question, particularly since Hayne (1949) found, when studying the home range of *Microtus pennsylvanicus pennsylvanicus*, that there was a positive relationship between the apparent size of the home range and the distance used between the traps. Others, however, including Blair (1951) and Stickel (1954) have found that ranges revealed by trapping were significantly related to the animal's natural range of movement and were not merely artifacts. Before considering the results of the data obtained from Silwood Park (Brown 1954), some discussion of definitions and methods of analysis of the movements of small mammals is advisable.

DEFINITIONS AND METHODS

Burt's (1943) definition of a true home range is widely accepted: 'that area about its established home which is traversed by the animal in the normal activities of food gathering, mating and caring for young. It excludes those areas traversed by vagrants or other individuals in search of home sites'. Other authors make reservations: for example Godfrey (1954*a*) omits 'about its established home': an important point since Blair (1951) has shown that for certain mammals 'an established home' is not necessarily an entirely permanent one. Territoriality is kept distinct from home range, a territory being any defended area: defence concerning mainly care of the young and provision of food and shelter. Trap revealed home range is described by Hayne (1949) as that area over which the animal enters the traps with greater or less frequency according to their location.

Various methods have been adopted, when live trapping records have been used to estimate true home range. The *Minimum Area* method (Dalke 1942, Mohr 1947) includes the areas connected by the straight lines that join the sites of capture and thus accepts as the animal's range of movement only that area within known points of capture. The *Boundary Strip* methods include also an area beyond the minimum area, either compensating for lack of traps at a boundary or acting as an area equidistant between two sets of traps. Experience has shown that it is difficult to determine exactly how much area should be included. Different methods will give different results from the same data. The *Inclusive Boundary*

Strip method (Blair 1940*a*) and the *Exclusive Boundary Strip* method (Stickel 1954) illustrate this point. Other methods based on different types of analysis also include an area beyond that of the minimum area. Among these are Manville's (1949) and one discussed but rejected by Godfrey (1954*a*). Both these methods will be considered more fully later. All the current methods of estimating home range from trapping data rely on the assumption that the animals do not normally travel to any important degree beyond the point at which they are captured (Hayne 1949). At the same time, however, there is the fact that direct conversion of linear measurements into area nearly always overestimate the size of the range (Godfrey 1954*a*). Again all these methods are only applicable under certain conditions, notably that of having sufficient records for the whole of the home range to be revealed. Blair (1942) found that for *Peromyscus maniculatus* ten or more captures were necessary in order to reveal the maximum home range. Godfrey (1954*a*), when allowing *Microtus agrestis* unrestricted movement, found that from sixteen to nineteen records from her Geiger counter apparatus were needed before maximum values of the home range were obtained. In view of the 'trap-shyness' of certain small mammals (Brown 1954) the majority of the animals captured do not allow of such analysis, but their movements can be considered by methods which involve distances between captures. *The Observed Range Length* method analyses the distances between most widely separated capture sites, whilst the *Adjusted Range Length* method adds half the distance to the next trap on to the observed range length. To test the validity of these methods Stickel (1954) applied them to artificial populations, and found that the *Exclusive Boundary Strip* method for measuring area and the *Adjusted Range Length* method gave sizes closer to the true range than did the other methods.

Hayne (1950) estimated a 'centre of activity' from all his points of capture and calculated home range from this centre rather than from any point of actual capture. Blair (1951) considers that a better term for such a point would be an 'average point of capture'. Hayne's fixed point is one computed from trapping data which is unlikely to be the animal's true centre of activity and does not allow for the fact that activity positions may change within the home range. Blair (1951) also criticizes Hayne's 'centre of activity' on the ground that equal probability of capture is assumed at equal distances from the centre of activity. Statistically this is a sound proposition, biologically it is not. Blair (1951) cites a pair of *Peromyscus polionotus leucocephalus* that spent most of their time at one corner of their home range and others that avoided certain parts within the home range. Davis (1953) likewise found that few mice used the whole of their home range. Instead they tended to follow more or less definite pathways. Yerger (1953) has emphasized that there is not such a thing as a fixed true home range but that it should be realized in using the term as Burt (1943) defined it, that any result obtained is true only for the period of time over which the experiment lasts. Among other things, the home range will be limited by the animal's ability, or necessity, to travel for food or protection and will be further limited by the seasons, the population density and by the animal's age and sex.

One of the most reliable ways of judging the validity of estimates based on trapping is to assess them alongside actual track records. Blair (1951) compared such results for beach mice, *Peromyscus polionotus leucocephalus*. He found that his results for home range from the trap records were fairly reliable when judged alongside the animal's tracks in the sand. Track observations added many facts that could not be obtained by a grid method of trapping. For example, tracks showed that the animal's movements were purposeful, involving definite journeys away from and back to their holes and were not vague meanderings occupying several hours. He found that the number of trails per mouse in one night varied from one to nine. Again Howard (1949) studying the snow tracks of *Peromyscus maniculatus bairdii* found that the mice usually went and returned by the same route. Movements of mice, either to new sites within the home range or less frequently outside it, were also observed by this method. Howard (1949) found that all the mice in one nesting box might, in the winter, move to another such box 500 ft away, or a female might move a similar distance before producing a litter. Such movements to new sites within the home range were a common occurrence for *Peromyscus polionotus* (Blair 1951). These mice kept a certain percentage of the holes within their home range in good condition. Blair estimated that some twenty mouse holes were, on an average, to be found in one animal's home range, and that of these about five were in use at any one time. When it was released from a trap, the mouse appeared well orientated within the home range and showed little hesitation in entering any of these holes. In fact the mouse had an entrance available in several parts of the home range, but such holes were more than refuges since the mouse might choose to change from one hole to another for its major activities of feeding and breeding. New holes were constantly being formed. Seven of the mice had in the spring abandoned 75% of the holes used in the autumn and 28% of the holes they were using were new.

In spite of this movement within the home range, and the fact that there may be a dispersal before settlement, once a definite home range is established the mouse is likely to remain there, or in its vicinity, for life. The choice and maintenance of the site are governed by many factors including availability of food and cover. Blair (1951) found that changes in the population of beach mice resulted principally from the immigration and settlement of young mice, and from the disappearance of resident adults. Howard (1949) found that the dispersal movements of *Peromyscus maniculatus*, which might be as much as 3300 ft, usually occurred as the young individuals became sexually mature. Other individuals, however, set up their residence within the area of their birth. Dice & Howard (1951), when studying *Peromyscus maniculatus*, found that of seventy-one females and sixty-four males 38% of the females and 28% of the males remained in their natal home range. Dispersal for most individuals occurs only once just before breeding, and this period of establishing residence in a new area appeared to be a critical one for the animal. Dispersal was not at random, both the 'stay at homes' and those dispersing large distances were greater than would be expected by a random curve. Dispersal has, on the other hand, not been shown for

all small mammals. Godfrey (1953, 1954*a*), for example, found no evidence that *Microtus agrestis* L. dispersed far from its place of birth. Of twenty-one voles that were immature when first trapped, only two were taken more than 30 yd from the original position. Since she admits that one of the disadvantages of her method was that large numbers of the marked mice were not recaptured, she may have been dealing only with that percentage of the population that remained within the natal site. On the other hand, behaviour of the population of *Microtus* at Silwood Park (Brown 1954) could best be explained if migration occurred in this species.

In general, therefore, present knowledge suggests that for certain small mammals, after sexual maturity is reached, the animal has settled down to take its place in a more or less fixed community. The actual position of residence within the home range may vary but no large-scale movement from this position is likely to occur other than 'occasional sallies' from which it will return. Blair (1951) observed a pair of beach mice and found that in contrast to the 822 times that they went into their holes in their established range, they went during the same period only thirty-five times outside it. Recognizing the fact that a home range is not a rigidly fixed area, and admitting the limitations of trapping to reveal details of its use, is there any value in estimations that are based on a grid system of trapping? Whilst opinions differ, Blair (1951) considers that although it gives only a crude estimate, it is by far the best one yet in use. He himself takes certain precautions in moving traps to prevent the mice getting too familiar with them. Other precautions are widely recognized. An optimum number of traps must be chosen, to allow for the presence of at least two for the home range of each animal. Too few may cause failure to catch the mouse, too many may mean that the animal is caught before it has reached the limit of its range. Dice and Howard (1951) consider that Blair's (1940*b*) estimate for the home range of *Peromyscus maniculatus bairdii* (2·29 acres) was too small, owing to too close trapping. Again, sufficient records must have been taken to ensure that the maximum range has been covered, although in view of the fact that the mice may not use all the 'range' this is to some extent an impossibility. It has also to be recognized that the traps themselves may influence movement. Following sand trails of beach mice, Blair (1951) tracked a female that visited a line of traps for 560 ft, visiting each trap in turn. Such a mouse may, however, be an exception. Stickel (1948*b*) found that for *Peromyscus leucopus* it was safe to assume that the animals remained within their home range, even though additional traps were available beyond it. Trap-shyness has also to be considered (Brown 1954, Godfrey 1954*a*). However long the period of investigation, the animal may be captured few times for this reason alone. Blair (1951) believes that the criticisms made by Hayne (1949) and Howard (1949) apply chiefly to the conditions when traps are left set for an extended period so that the animal remains trapped for too long and is unable to move to the limits of its range. Blair (1951) found that in fact, the animals tended to range more widely than trap records alone would show. For seven male beach mice the trap-estimated home range was 5·98 acres, whereas a track-estimated range was 8·30 acres.

MOVEMENT OF *MICROTUS AGRESTIS*

Bearing in mind the observations and criticisms reviewed above, the data obtained whilst trapping at Silwood Park 1949-51 (Brown 1954) are analysed in a number of ways that are judged to give interesting results concerning the movements of the three species: *Microtus agrestis hirtus* (Bellamy), *Apodemus sylvaticus sylvaticus* (Linnaeus) and *Clethrionomys glareolus britannicus* (Miller). Certain of the methods allow the data of a large number of animals to be considered, in contrast to attempts at estimating home range which involves dealing with only that section of the small mammal community that enters the traps a large number of times.

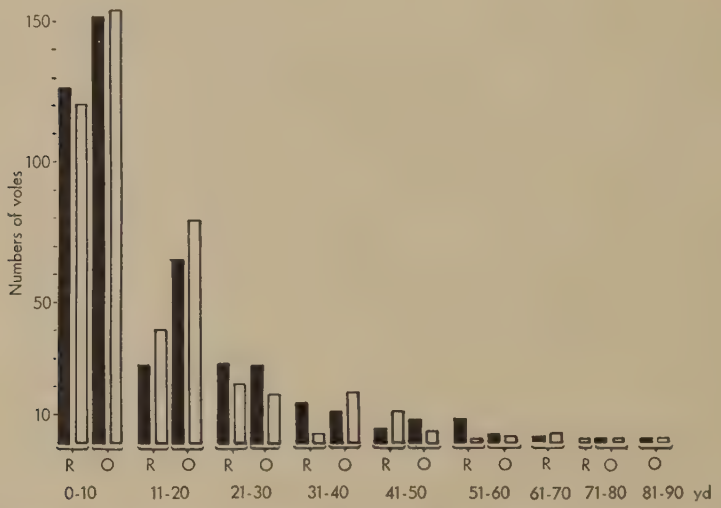

Fig. 1. Analysis of the maximum movement recorded for each retrapped *Microtus agrestis* during trapping periods from September 1949 to September 1951. Maximum movement is taken as the greatest distance the vole travelled from its point of capture on one day, to that of the next day of capture. R, Rookery Slope; O, Observatory Ridge; ■, males; □, females.

Microtus agrestis hirtus was trapped in two areas of rough grass land, using traps at 10 yd intervals (Brown 1954). To prevent voles from building their runways up to the entrance, the traps were moved each day within the quadrat. Fig. 1 analyses the maximum movement made by each individual in passing from its point of capture on one day to that of the next day of capture. Such a movement might occur at any time during the trapping period of 10-14 days. On the two areas, Rookery Slope and Observatory Ridge, the behaviour of the two voles was similar. 57·95% of the males and 57·85% of the females never moved more than 10 yd, as far as the trapping records were concerned, since they were always recaptured at one particular trap, within the same quadrat. A further 41·25 % of the males and 40·7% of the females never moved more than 60 yd and

only 0·8% of the males and 1·45% of the females moved between 61 and 90 yd. That the area of movement of *Microtus agrestis* is a restricted one has also been shown by Chitty (1952) and Godfrey (1954*a*). Chitty found that the number of movements greater than 10 yd was so small that no analysis according to age and sex could be made. Two exceptional distances of 42 yd and 110 yd were recorded for adult males and one distance of 70 yd for an adult female.

Fig. 2 summarizes every movement, as judged from one point of capture to the next, made by each *Microtus* that was trapped on successive dates of capture. In all there were 1135 movements made by the males and 1131 such movements made by the females. Only movements of less than 10 yd were recorded for 57·35% of

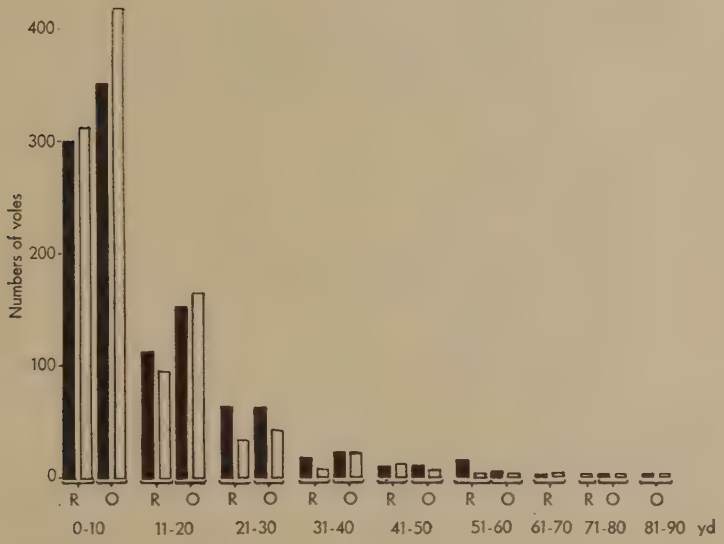

Fig. 2. Analysis of every movement of *Microtus agrestis*, within each trapping period, judged from one point of capture to the next. (For symbols see Fig. 1).

the males and 64·54% of the females. 42·64% of the males and35·45% of the females moved distances between 11 and 60 yd and those animals that moved between 60 and 90 yd on any one night of trapping represented on 0·006% of the males and 0·005% of the females. Of the 222 males and 201 females that were captured on Rookery Slope only 24 males and 24 females were trapped five or more times during any one trapping period. Similar figures for Observatory Ridge are 31 males and 28 females from totals of 266 males and 276 females. These voles, with five or more recaptures have been selected for further study. Their observed range length (the greatest distance between any two points of capture) are on Rookery Slope averaged at 30·9 yd (range 10-55 yd) for the females and at 40·0 yd (range 10-62 yd) for the males. Figures for Observatory Ridge are very similar:

females 29·1 yd (10-45 yd) and males 39·3 yd (10-70 yd). Adjusted range lengths will be five yards greater than those given above.

In view of the fact that for some of the animals, the number of recaptures was small, Manville's (1949) method was chosen to give an idea of the trap-revealed range of movement of these animals. Their revealed range was judged as the area of the quadrats into which the voles actually moved, or through which they must have passed to get, for example, from area A to area C necessarily transversing area B. Fig. 3 analyses these results and shows firstly that there is some tendency

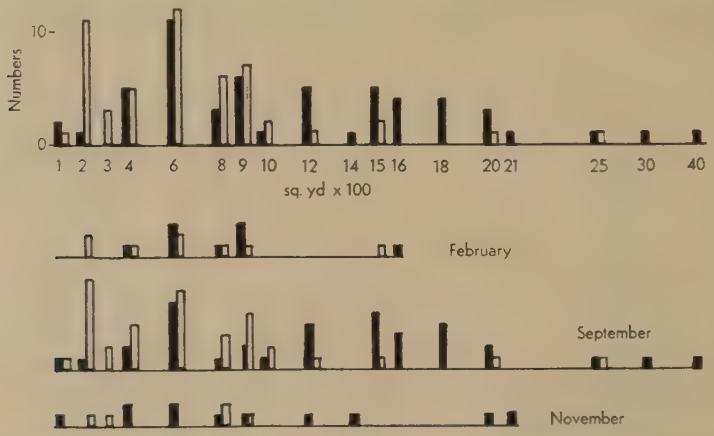

Fig. 3. The range of movement of *Microtus agrestis* as revealed by trapping (Manville's 1949 method). ■, males; □, females.

for certain of the males to wander further than the females. This fact is well established in many species of mammals, but it does not necessarily mean that there is a significant difference in the sizes of the home range of the two sexes (Blair 1951). Secondly, Fig. 3 shows that there was somewhat more movement of these voles in September than in February or November. No voles were captured on these areas in June 1950. It would have been interesting to have trapped during April or May to have checked whether *Microtus* shows signs of dispersal movements as sexual maturity is reached, as is reported for many young mammals (Blair 1940*a*, Evans & Holdenried 1943, Errington 1944, Howard, 1949). Godfrey (1953), checking the movements of *Microtus* by means of radio-active material, found no evidence for such dispersal in an area bounded by habitats that were unsuitable for *Microtus*. At Silwood Park the areas examined lay within extensive grassland which would have provided no obstacle for such movements. Complete absence of voles in June, followed by good populations in the autumn, certainly suggest that dispersal movements do occur in such areas.

Manville's method (Fig. 3) gives an average range of movement of the selected *Microtus* as 1162 sq. yd for the 55 males and 600 sq. yd for the 52 females. These figures compare favourably with those of Blair (1940*a*) for *Microtus pennsylvanicus*

pennsylvanicus (968-1210 sq. yd). Godfrey (1954*a*), working with *M. agrestis* gives in her Table 1, the length of the distances marking furthest points of location for each of twenty-three animals (one male and twenty-two females), and gives as breadth the distance in yards between the two furthest points at right angles to the first measurement, though not necessarily through the mid point. These points were usually the diagonals of a parallelogram. Had she multiplied these two results together then the method would have been similar to that of Manville (1949), but not identical; her range for *M. agrestis* females would have been 200-980 sq. yd with an average of 500 sq. yd (comparable average for the females at Silwood Park was 600 sq. yd). Godfrey considers that such a method of calculation would give results that are undoubtedly too large. Whilst one agrees that direct conversion of linear measurements into areas may overestimate the size of the range, several other points need consideration. Was there any strict biological reason for the breadth of the ranges of her voles to be consistently much less than the length? For the 107 animals from Silwood Park, fifty-nine had ranges whose lengths were greater than their breadth, thirty-one ranges were more or less square and seventeen had breadths greater than the length. Secondly it is open to question whether when a human being is moving about an area vole behaviour is completely normal. Whilst on the other hand it can be argued against trapping that distance may be exaggerated because of attraction to traps, yet there is also the evidence that when trap and track estimates are compared simultaneously, ranges from the former may be less than from the latter (Blair 1951).

Stickel (1954) found that the exclusive boundary strip method gave the best results when applied to artificial populations. Godfrey (1954*a*) used the minimum area method which Stickel judged to be too small. Using the exclusive boundary strip method for the Silwood Park figures an average range of 1185 sq. yd (300-3400 sq. yd) is obtained for the males and 781 sq. yd (300-2000 sq. yd) for the females. The minimum method gave an average of 535 sq. yd (100-1800 sq. yd) for the males and 462 sq. yd (100-1400 sq. yd) for the females. Manville's method and the exclusive boundary strip method will in this instance be seen to give very similar results. It is obvious, however, from these calculations that the particular statistical method employed for judging the animal's range of movement can cause much variation in the results that are obtained from the same data. Since the data from Silwood Park come from animals that were trapped a small number of times it could be judged that the resultant ranges would be too small, as there would not have been sufficient records to cover the whole range. Analysis of times of capture during any one trapping period are as follows. Males: 16 caught 5 times, 17 caught 6 times, 8 caught 7 times, 7 caught 8 times, 2 caught 9 times, 4 caught 10 times and 1 caught 11 times. Females: 16 caught 5 times, 18 caught 6 times, 9 caught 7 times, 6 caught 8 times and 3 caught 9 times. All the males that were caught eight or more times had ranges exceeding 950 sq. yd (exclusive boundary strip method). With two exceptions of 450 and 500 sq. yd all the females caught eight or more times had ranges exceeding 750 sq. yd (exclusive boundary strip method). These analyses are, however, dealing with only a small percentage of the popula-

tion and it would not be correct to assume that voles that were more trap-shy necessarily had ranges of a similar size. On the other hand, the voles at Silwood appeared to have a somewhat wider range of movement than did those studied by Godfrey (1954*a*) at Wytham. In spite of small numbers of captures, length and breadth of range for nearly all the animals caught six times or more at Silwood were greater than those at Wytham. Fig. 4 illustrates this point for a few of the Silwood voles.

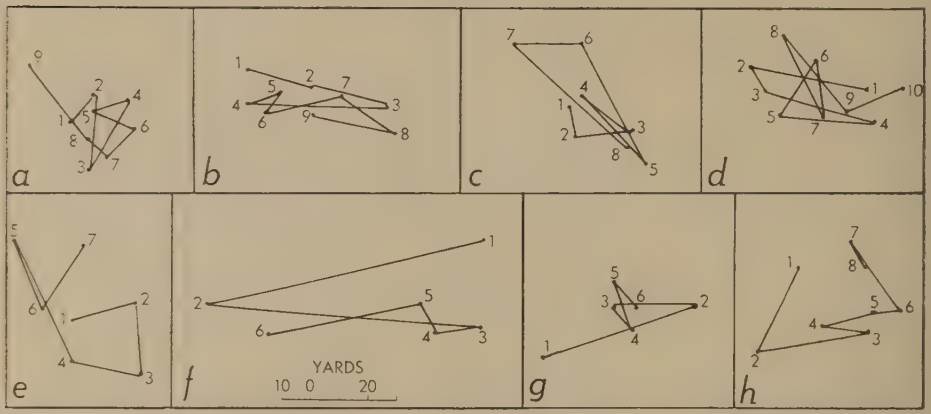

Fig. 4. Points of capture of selected *Microtus agrestis*. The following figures for trap-revealed range (sq. yd) are based on Manville's (1949) method:

a, 1600, male, September 1951
b, 1800, male, September 1950
c, 2000, male, September 1949
d, 2400, male, September 1950
e, 2500, female, September 1949
f, 4000, male, September 1950
g, 1800, male, September 1950
h, 2500, female, September 1949

Blair (1951) discusses the fact that species of *Peromyscus* take up residence for a period in different parts of their home range. The points of capture of the voles at Silwood were examined to see if there was any evidence of a similar occupancy of different holes within the home range, or whether an entirely new range had been adopted. When a single trapping period was considered, although there were a number of examples where a vole was caught in one position a number of times and then persistently caught some distance away, there was not enough evidence to establish the fact that the vole had changed residence. The points of capture of voles that were taken during more than one trapping period were examined. On Observatory Ridge four animals appeared to have moved their homes (Fig. 5). Of 86 recordings of retrapped animals 15 males and 23 females were captured in exactly the same area as previously, 15 males and 12 females were caught within 10-20 yd, 10 males and 7 females were caught within 20-30 yd and 5 males within 40 yd of the original area of capture. In none of these cases was there any reason to judge that the vole had moved out of its original home range. Often there were too few original captures to have assessed the true range of movement of the vole at the first trapping period, or to have decided if one distant capture was strictly

within the animal's range (e.g. Fig. 5, Nos. 1 and 5). On Rookery Slope, three males may have moved their homes (Fig. 5, Nos. 5-7). Of the others that were recaptured in more than one trapping period 8 males and 11 females had not moved more than 10 yd, 4 males and 3 females had not moved more than 20 yd, and 4 males and 3 females had not moved more than 30 yd. If occasional sallies or movement of homes are not the explanation for the positions of capture of animals 1-7 in Fig. 5 then their home ranges are exceptionally large. The more typical picture of the behaviour of the majority is seen in the points of capture of the one vole (a female, Fig. 5, No. 8) that was captured in four successive trapping periods.

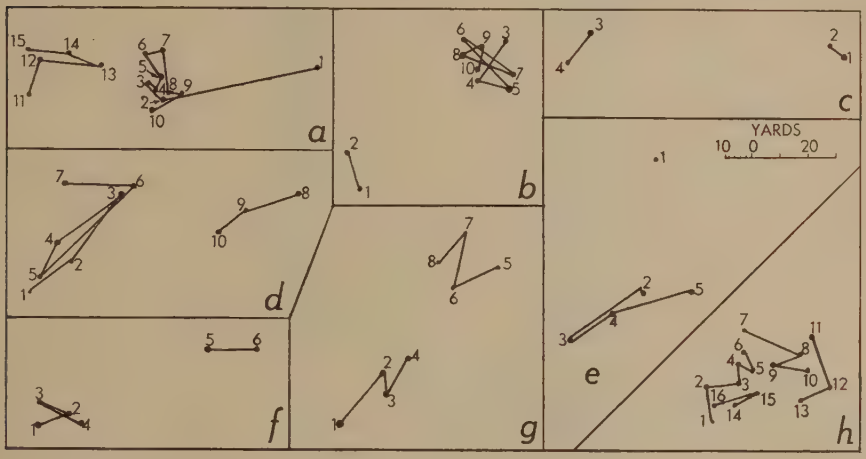

Fig. 5. Points of capture of *Microtus agrestis*:

	Animal No.	Sex	Successive points and months of capture	
a	1	♂	Observatory Ridge	1-10, Nov. 1949; 11-15, Feb. 1950
b	2	♂	,, ,,	1-2, Sept. 1950; 3-10, Mar. 1951
c	3	♀	,, ,,	1-2, Sept. 1949; 3-4, Nov. 1949
d	4	♀	,, ,,	1-7, Sept. 1949; 8-10, Nov. 1949
e	5	♂	Rookery Slope	1, Sept. 1950; 2-5, Mar. 1951
f	6	♂	,, ,,	1-4, Sept. 1950; 5-6, Nov. 1950
g	7	♂	,, ,,	1-4, Sept. 1950; 5-7, Nov. 1950
h	8	♀	Observatory Ridge	1-6, Sept. 1950; 7-10, Nov. 1950; 11-13, Mar. 1951; 14-16, June 1951

Animals 1-7 are judged to have moved their home ranges from one trapping period to the next No. 8 shows the more usual points of capture of a vole during successive trapping periods.

MOVEMENT OF *APODEMUS SYLVATICUS* AND *CLETHRIONOMYS GLAREOLUS*

Similar records are considered for *Apodemus sylvaticus* and for *Clethrionomys glareolus* trapped in a mixed woodland (South Lodge Wood), where traps were placed, in groups of four, 30 yd apart (Brown 1954).

Fig. 6 gives the maximum movements of each animal during a single trapping period for mice that were retrapped at least once. It shows that under the condi-

tions of the experiment, few animals moved any great distance in the wood. This may have been partly due to the fact that there were wide areas under beech trees that provided very poor cover for a small mammal. 68·5% of the male *Apodemus* and 65·1% of the male *Clethrionomys* moved less than 30 yd. Similar figures for the females are 71·5% and 60·4% respectively. Those that moved 91-120 yd were all males: 0·16% *Apodemus* and 0·33% *Clethrionomys*. Under different experimental conditions male *Apodemus* move far greater distances (Chitty 1937, Hacker & Pearson 1951), but these live trapping experiments were not designed to test the maximum homing ability of the mice.

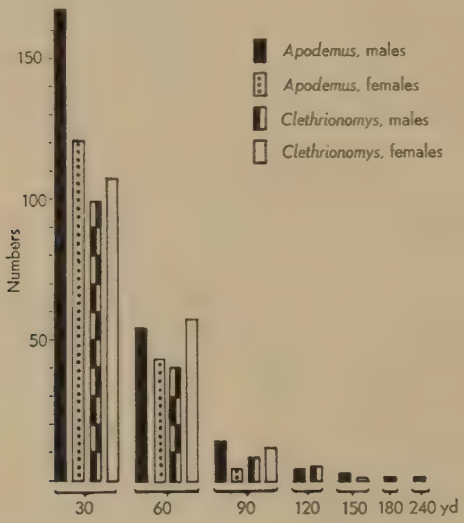

Fig. 6. Analysis of the maximum movement recorded for each retrapped *Apodemus sylvaticus* and *Clethrionomys glareolus* during trapping periods from September 1949 to June 1951 (see Fig. 1).

Fig. 7 analyses the total movements of the *Apodemus* and *Clethrionomys* that were recaptured at least once during a trapping period and again shows that there was little movement of mice from one set of traps to another. Only males moved more than 150 yd and such animals represented much less than 1% of the total.

The animals that were trapped five or more times were again considered in greater detail. Table 1 summarizes the results.

There was less marked seasonal difference of movement for these two small mammals (Fig. 8) than there was for *Microtus*. Three male *Apodemus* that moved over areas of 9000 and 14 400 sq. yd did so during the autumn months. In general, *Apodemus* moved further than *Clethrionomys* and males further than females. Chitty (1937) had found that 82% *Apodemus* and 74% *Clethrionomys* moved less than 30 yd, when traps were spaced at 5 yd intervals. He considered that these

distances were controlled, to some extent, by the close spacing of the traps and found distances of movement were greater when the traps were moved further apart.

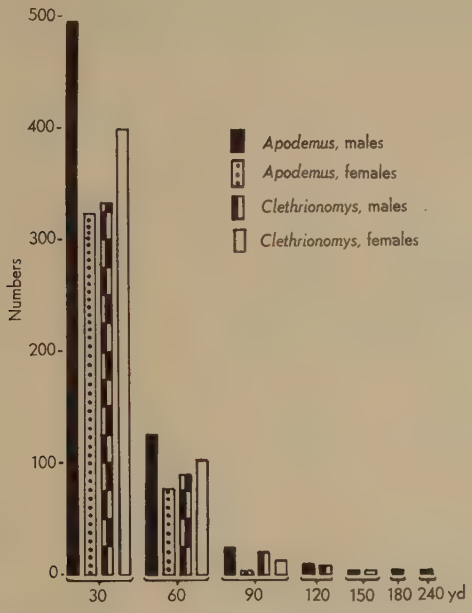

Fig. 7. Analysis of every movement made by *Apodemus sylvaticus* and *Clethrionomys glareolus*, within each trapping period, as judged from one point of capture to the next.

Table 1. *Summary of observations in South Lodge Wood*

	Apodemus sylvaticus		*Clethrionomys glareolus*	
	males	females	males	females
Numbers studied	211	201	155	172
Trap-revealed ranges (sq. yd) of animals caught >5 times: Number of animals	39	25	34	35
Manville's (1949) method — average	3092	2628	2144	1697
Manville's (1949) method — range	900-14 400	900-8100	900-5400	900-5400
Exclusive boundary strip method — average	4744	4280	3602	2571
Exclusive boundary strip method — range	1100-14 000	1100-9500	1000-8500	800-7600
Minimum area method — average	2666	2168	2002	1545
Minimum area method — range	900-8000	700-4500	800-3600	600-3000
Percentage trapped in only one quadrat (900 sq. yd)	68·5	71·5	65·1	60·4
Trap-revealed movements judged from one day to the next (%) — <30 yd	73·6	80·1	74·0	77·2
Trap-revealed movements judged from one day to the next (%) — <60 yd	92·2	99·0	94·0	97·1
Trap-revealed movements judged from one day to the next (%) — <90 yd	95·8	100·0	98·4	99·4
Observed range length (yd) — average	64·6	57·6	59·1	48·0
Observed range length (yd) — range	30-120	30-120	30-120	30-90
Observed range length (yd) — numbers studied	39	25	34	35

Manville (1949) studying *Peromyscus*, found that the adult males had a trap-revealed range of 500-1500 sq. yd and the adult females 600-1200 sq. yd. Proportionately smaller areas were covered by the juveniles. These figures were somewhat lower than those of Burt (1940) for *P. leucopus* and of Blair (1942) and of Dalke (1942) for *P. maniculatus*, and for *Apodemus sylvaticus* (Table 1).

Fig. 8. The range of movement of *Apodemus sylvaticus* and *Clethrionomys glareolus* as revealed by trapping (Manville's method).

During any one trapping period there was no evidence of either *Apodemus* or *Clethrionomys* moving to new positions within their home range or adopting a new home range altogether. The positions of recaptured animals, after periods of three months are now considered. Twelve of such male *Apodemus* (48%) were recaptured in the same area as previously. Seven of them (30%) were found in adjacent quadrats. Of the remainder, three were trapped within 90 yd of their original point of capture and only two young animals had moved more than 150 yd away. The position of these two animals and of one other are shown in Fig. 9 (*a*, *b*, *c*). Too few captures are available to make definite statements, but there is a likelihood that these three animals had changed their homes. Twelve of the female *Apodemus* (54·5%) were recaptured within the original quadrat, nine (41%) were recaptured in an adjacent quadrat and one animal was recaptured 85 yd from its first position of capture. 67% of both the male and female *Clethrionomys* (12 and

18) were recaptured in the same quadrat. 17% of the males and 22% of the females were recaptured in an adjacent quadrat and one male was recaptured 85 yd away. Two young males and one young female (Fig. 9, *d*, *e* and *f*) were recaptured at greater distances, over 150, 180 and 210 yd away respectively. It will be noted that all the large-scale movements shown in Fig. 9 occurred in the autumn and winter.

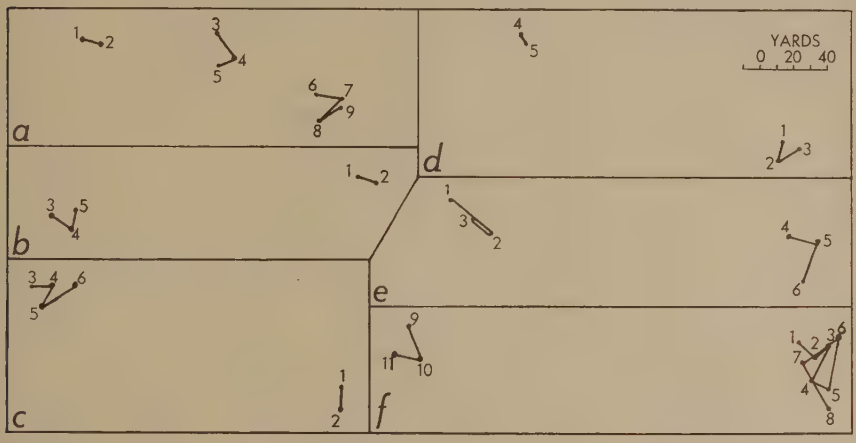

Fig. 9. Points of capture of animals that are judged to have moved their home range from one trapping period to the next.

a, *b* and *c*, *Apodemus* males: *a*, points 1, 2—Sept. 1949; 3-5—Nov. 1949; 6-9—Feb. 1950. *b*, points 1, 2 —Nov. 1950; 3-5—Feb. 1951; *c*, points 1, 2—Nov. 1950; 3-6—Feb. 1951. *d* and *e*, *Clethrionomys* males: *d*, points 1-3—Nov. 1949; 4, 5—Feb. 1950; *e*, points 1-3—Nov. 1949; 4-6—Feb. 1950. *f*, *Clethrionomys* female, points 1-8—Nov. 1949; 9-11—Feb. 1950.

DISCUSSION

Only a limited comparison can be made between the movements of small mammals at Silwood and those in other habitats. Differences in the environment, in experimental procedure and analysis all contribute to variations in the results. At the same time individuals within a community behave differently, some never venturing as far afield as others. Blair (1951) emphasized the extent of this variation in a community of beach mice, finding the animals could be grouped into sets whose home ranges varied from 1·97-10·66 ac. Similar variation at Silwood was such that the home ranges of *Apodemus* were from 0·23-2·87 ac for males and 0·23-1·98 ac for females.

When small numbers of animals are being studied only one section of the community may be involved. Different results for the movements of *Microtus agrestis* at Silwood as compared with Wytham (Godfrey 1954*a*, 1954*b*) may illustrate this point. Godfrey's radio-active detection method may have examined only those voles with small home ranges. The whole *Microtus* population of the area was not included because voles that occupied similar ranges could not easily be kept dis-

tinct with her apparatus. Godfrey's main analysis was for twenty-three animals (twenty-two females) whereas that at Silwood was for 423 animals. A selected number of *Microtus* at Silwood would have given, as an average between two furthest points of location, a comparable distance with hers (19·04 yd) yet the *Microtus* that entered the traps most readily at Silwood had average observed range lengths of 40·0 yd for males and 30·9 yd for females. Comparison is again limited, however, since Godfrey's twenty-two females need not have come from that section of the community that most readily enters the traps (Brown 1954).

At Silwood unless the *Clethrionomys* remained indefinitely under a particular group of shrubs many were forced to move some distance across beech humus to new cover. This environmental reason may in part explain why the home range of *C. glareolus* at Silwood was 0·21-1·8 ac for males and 0·17-1·57 ac for females as compared with an average of 0·15 ac for *C. smithi* (Tanaka 1951). The observed range length of selected *C. glareolus* was 50·3 yd compared with 26·3 yd for *C. smithi*. Environmental differences influencing the amount of movement of *C. gapperi* were reported by MacLulich (1951). Breeding females averaged 51 yd in spruce, white pine and birch forest compared with 120 yd in hemlock, yellow birch and sugar maple forest. *Peromyscus* similarly shows environmental influence on the amount of its movement (Stickel 1948*a*, for *P. leucopus* and Blair 1951, for *P. polionotus*). The movement of *P. maniculatus* as reported by Dice & Clark (1953) was of the same order as that for *Apodemus sylvaticus* at Silwood. In both cases over 50% of the mice moved less than 60 yd and distances beyond 80 yd were exceptional. Similar results were obtained for *Peromyscus* by Howard (1949), Blair (1951) and Stickel (1954). The latter found that only a small proportion of the mice travelled between traps. At Silwood, by comparison, 70% of the *Apodemus* were captured in one position only. Manville (1949) found the maximum distance travelled in one day for *Peromyscus* was, on the average, 84·3 yd for males and 79·6 yd for females. This is higher than the observed range length for *Apodemus* (64·6 yd for males and 57·6 yd for females).

The trap-revealed range of *Microtus agrestis* at Silwood, using the minimum area method, ranged from 0·06-0·70 ac, averaging 0·24 ac for males and 0·16 ac for females. These are higher averages than the 0·05 ac obtained, for the same species, by Godfrey (1953) in experiments not involving traps. Hayne (1950), Blair (1940*a*) and Stickel (1954) have all studied the home ranges of *Microtus pennsylvanicus*. Their results do not show any wide variation one from the other but whilst Hayne believes that trapping experiments show only the complex relationship between animal and trap, Blair (1951) and Stickel (1954) are of the opinion that results from trapping experiments give reliable information concerning the movements of small mammals, having compared such results with those obtained by other means. Stickel has shown that there is an optimum spacing for traps, but this is not known for each species, but only as yet for artificially prepared populations.

Experiments at Silwood gave little evidence of dispersal of voles and mice. There were a limited number of animals, of each of the three species, that appeared

to have moved to a new home range. Two young male and one young female *Clethrionomys* moved 150-210 yd. Manville (1949) found dispersal distances for *C. gapperi* to be between 50 and 120 yd for males, 45 and 50 yd for females and 90 and 103 yd for juvenile males. Distances of dispersal are influenced by a great number of factors, all controlling population pressures. Once a home range is established there is, however, a tendency for the animal to remain within it, or its vicinity, for life. In fact species of *Apodemus* and *Peromyscus* are among those mammals well known for their true homing ability. Murie & Murie (1931, 1932) found that *Peromyscus maniculatus* returned to its home site when released at distances up to two miles. Hamilton (1937, 1939) reports results of a similar nature for *Peromyscus leucopus*, but he found this homing ability far less marked in *Microtus*.

To what extent do small mammals move from one home to another within their home range? This will vary both with the species and with the habitat. Blair (1951) considered the behaviour of beach mice to resemble a miniature type of nomadism; they moved continually to new holes, often some distance from one another, within their home range. A similar formation of new holes was studied at Silwood for rabbits but no detailed observations were made for small mammals. *Apodemus* and *Clethrionomys* would probably have had little opportunity of this type of movement when their populations were high. They lived mainly under trees and shrubs and appeared to use existing holes rather than make new ones. A strange *Apodemus* that was introduced into South Lodge Wood during a 'homing' experiment appeared unable to settle there; it occupied the traps rather than venturing down to the homes of the other animals. Other *Apodemus* moved into open grassland that was comparatively free of *Microtus* and stayed there for over a year until the *Microtus* population increased again. The availability of homes within an area is just one example of the many varying biological factors influencing the animal, making precise concepts of its movements extremely difficult.

ACKNOWLEDGMENT

A grant from the University of London Central Research Fund provided assistance during 1950-51.

SUMMARY

1. The movements of *Apodemus sylvaticus sylvaticus*, *Clethrionomys glareolus brittanicus* and *Microtus agrestis hirtus* have been examined in various ways from data obtained during 'mark and release' live trapping experiments.

2. Averages of trap-revealed ranges (Manville 1949) for males trapped five or more times were for *Apodemus* 3092 sq. yd, for *Clethrionomys* 2144 sq. yd and for *Microtus* 1162 sq. yd. Females occupied proportionately smaller areas. Results of home ranges using the minimum area method and the external boundary strip method are also considered.

3. Behaviour in the populations examined was not uniform. 'Stay at homes' and 'wanderers' were both present, contributing to a wide range in the types of movement examined. A larger proportion of the animals, however, showed restricted activity. Taking as an estimate of movement the distance between captures from one day's trapping to the next, 73% of the *Apodemus* and *Clethrionomys* moved less than 30 yd and 92% moved less than 60 yd, 55% of the *Microtus* moved less than 10 yd and 92% moved less than 30 yd.

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BALANUS BALANOIDES (L.) IN THE FIRTH OF CLYDE: THE DEVELOPMENT AND ANNUAL VARIATION OF THE LARVAL POPULATION, AND THE CAUSATIVE FACTORS

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(With 1 Figure in the Text)

The factors influencing the development and ultimate survival of the planktonic stages of those sedentary marine animals with a more or less extended planktonic phase in their life-cycle are of paramount importance in any consideration of the maintenance or spread of such a species. This view has recently been stressed by Thorson (1946). Under optimal conditions there is a progressive development of the larval population from stage to stage and it should be possible to follow the sequences quantitatively if adequate sampling techniques are employed. The ultimate spatfall will be a function both of the initial larval input and of any changes in numbers during the larval development. The larval input will vary from year to year; it will be affected by changes in the numbers of the parent population as well as its viability. We are not concerned here with such differences but propose to confine our attention to marked variations in the progress of the development of the larval population from one year to another in the cirripede *Balanus balanoides*.

In studies of this type, which extend over a number of years it is quite impracticable to follow all the possible variables which could be considered *a priori* to affect the larval population in question: the best that can be done is to collect as much information as possible and then, from this, to attempt to elucidate those factors of importance.

COLLECTION OF THE INFORMATION

There is a fairly extensive set of data collected over a number of years during the spring on the progress of development of the larval population of *B. balanoides* in the Clyde Sea Area. The normal pattern here is for Stage I nauplii (rapidly passing to Stage II) to appear in the plankton at about the time of the spring phytoplankton outburst; that is, during the early weeks of March. The major period of this liberation may be restricted to a few weeks, sometimes with the peak production taking place over an even shorter period. Beyond Stage II each further nauplius stage takes about three to four days before moulting, so that the cyprids appear three to four weeks after the liberation of the Stage I nauplii.

Pyefinch (1948) has given some data for the years 1944-47 and although, as he

points out, his collecting technique was inadequate for a proper quantitative assessment of larval numbers (quite apart from errors due to inshore sampling with consequent bias as regards the numbers of the earliest stages) his results certainly permit an assessment of the gross changes in the sequence of events from one year to another to be made.

Sampling in more recent years has been carried out in the centre of the Fairlie Channel, standard tows of a mile and a half being taken as far as possible each day during the spring weeks. In 1949 only a limited number of collections were made with a modified Hardy Plankton Recorder; the work was subsidiary to experiments on the performance of this instrument. In all later years collections have been made with a Hardy Plankton Indicator. The model used was that termed the 'standard' indicator by Glover (1953) and this, when towed on its 60 m of wire warp, samples at a depth of between 6 and 10 m. It has already been shown that the filtration coefficient of this machine is only slightly less than unity (Barnes 1951), that is, the gauze area is not quite sufficient to pass all the water reaching the nozzle; even so, in the absence of clogging, the results are comparable throughout all the series. Clogging during a diatom increase will, of course, reduce the catch. It should also be pointed out that evidence from other unpublished results indicates that there is no marked gradient in the larval populations of *B. balanoides* between 0 and 10 m, and the samples may be considered reasonably representative of the population in the upper levels.

After bringing the indicator inboard the catch was always carefully washed off the gauze and preserved; it was subsequently examined without sub-sampling. All the *B. balanoides* larvae were counted, and at the same time notes were made on the other zooplankton species present and their abundance assessed. The species of diatoms were also noted and although the gauze was inadequate for anything approaching a quantitative assessment of their numbers an estimate of their abundance was made. Frequently additional qualitative net hauls were taken during the season. In addition, Dr S. M. Marshall has contributed information on the species and numbers of diatoms present during some of the years under survey. The records of spring spawning herring in the area were extracted by Mr B. B. Parrish.

The methods employed in obtaining the physical and climatological records have already been given in detail (Barnes 1955). These records were extracted in greater detail for the spring months. In the absence of wind records prior to 1949 those for Prestwick, which is probably the most comparable nearby situation, have been used.

LARVAL FLUCTUATIONS, 1944-54

(*a*) *1944-47* (*see Pyefinch 1948*)

The years 1944 and 1945 seem to have been normal; there were heavy hauls of the early nauplius stages during March followed by a gradual transition to the

later stages of nauplii, and these ultimately gave rise to moderate hauls of cyprids in early April. The diatom outburst, largely *Skeletonema costatum*, the typical diatom of the spring outburst in the Clyde, took place during the early stages of larval development, was of moderate intensity, and was virtually over by 20 March In 1946 the sequence began in the same way and at much the same time, but the population did not develop; there was an almost complete absence of late stage nauplii and cyprids at the time when they would have been expected, namely during late March and early April. Pyefinch noted that in this season heavy hauls of diatoms persisted well into April and this observation led him to suggest that the absence of late stage nauplii and cyprids was in some way the result of the deleterious effect of the prolonged diatom outburst.

1947 was a more or less normal year as regards the cirripede outburst and late stages were succeeded by moderate numbers of cyprids. However, as in 1946, diatoms persisted well into the beginning of April, and Pyefinch therefore suggested that the inimical effect of the continued diatom production, postulated to explain the 1946 results, had been masked by a greater initial larval input.

(*b*) *1949, Hardy Plankton Recorder* (*see Barnes 1950*)

The results for this season were obtained incidentally to work on the behaviour and filtering capacity of the Plankton Recorder and Indicators, and some details of the results have already been given. The season was quite normal; a large population of all stages of nauplii developed in regular sequence and yielded a good cyprid population which was followed by an extremely dense settlement on the shore (Barnes & Powell 1950). There was a heavy diatom outburst consisting almost entirely of *Skeletonema* which began on 10 March, reached its maximum between 22 and 25 March, and was virtually over by the end of the month. The diatom maximum occurred therefore during late nauplii and cyprid development and there was no evidence that the coincidence had any deleterious effects upon the development of late stage nauplii or cyprids; indeed the results indicate that between Stage III and cyprids the larval population remained remarkably constant and unaffected by any possible disturbing factors.

(*c*) *1950-52, 1954, Hardy Plankton Indicator Fig.* (*1*)

The 1950 season was again normal, a moderate larval input being followed by a moderate production of late stage nauplii and cyprids again without any evidence of any gross depletion of the population. The diatom outburst (*Skeletonema*) began early in March (335 cells ml on the 14th) and there were some 3000 cells/ml on 25 March.

In both 1951 and 1952 the sequence of events was similar to that of 1946 in that the early stages did not give rise to a comparable late nauplius or cyprid population. Thus in 1951 304 Stage I-III nauplii per sample were obtained in early March at the first input peak, but this was followed by a serious depletion of the population, so that three weeks to a month later catches of only 2-5 cyprids per

sample were obtained. *Coscinodiscus* sp. were present during late February and *Chaetoceros* sp. became abundant during early March, but the diatom numbers

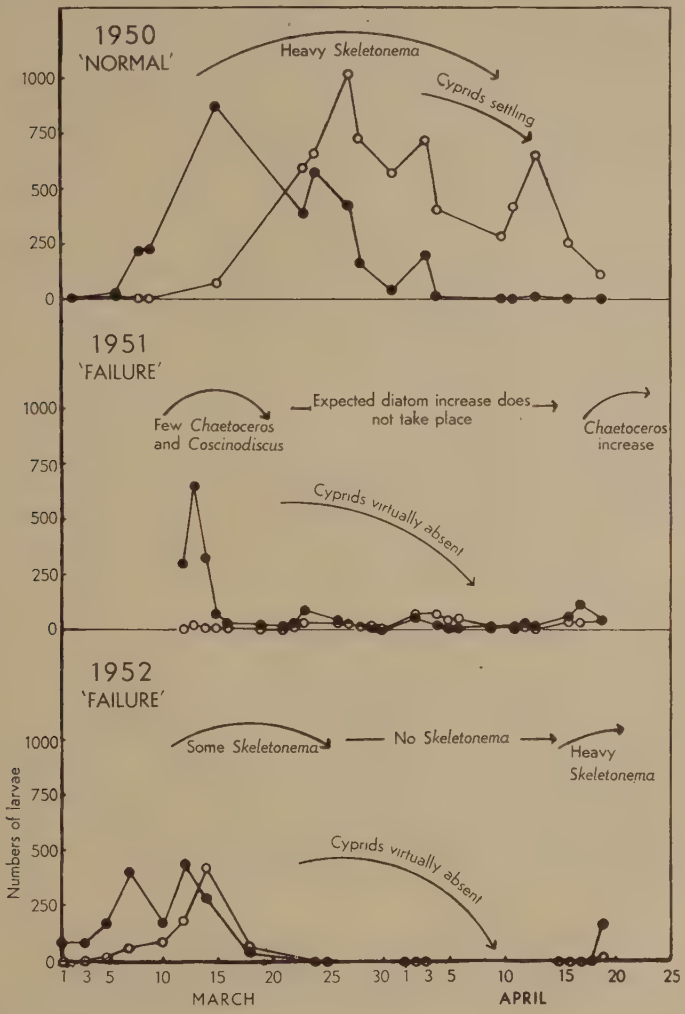

Fig. 1. Typical 'normal' and 'failure' years. *Balanus balanoides* larvae in 'daily' plankton hauls taken with the Hardy Plankton Indicator towed at standard depth over distance of 1½ miles in the Fairlie Channel. Quantitative data on diatom abundance are also given.
—●— Stages I, II and III.
—○— Stages IV, V, VI and cyprids.

then fell off suddenly so that few were present during the latter part of March. Although there was a distinct increase in *Chaetoceros* in mid-April the major outburst of *Skeletonema* was delayed until 10 May, after which *Thalassiosira* became relatively abundant.

In 1952 the early stage nauplii were present in numbers at a rather earlier date than usual, and at the same time there was a small outburst of *Skeletonema*; neither population developed. The diatoms disappeared almost completely and whereas 100 Stage I-III *Balanus balanoides* nauplii were present per sample in March only five cyprids per sample were obtained later in the season.

In 1954 only a limited number of quantitative runs were made but it was quite clearly another abnormal year. There was an initial production of nauplii which was again accompanied by a small outburst of *Skeletonema*, but, as before, neither population developed. In addition to the few quantitative samples, qualitative hauls were taken with ordinary tow nets and some vertical hauls for other experiments. There was an almost complete absence for some weeks of *Balanus balanoides* nauplii in any of these samples, and the virtual absence of diatoms at this time was clearly demonstrated by the pigment extraction method, for which samples were taken in connection with other work. A later liberation of nauplii eventually took place, concurrently with a sharply defined *Skeletonema* outburst; both populations developed normally.

The disappearance of the late stages and cyprids from the plankton in the 'failure' years was not the result of settlement on the shore. The failure years were marked by the paucity of the initial settlement. However, during such seasons a second and later outburst may take place when conditions are more favourable, e.g. during a relatively late diatom increase, and the success of this may to some extent mask an obvious correlation between failure years and overall density of settlement.

To summarize: in the 'normal' years (1944, 1945, 1947, 1949 and 1950) there was a steady development of the larval population from one stage to the next with good cyprid production and a good spatfall. In other years (1946, 1951, 1952 and 1954) the March outburst of *Balanus balanoides* nauplii failed completely at some stage in its development and cyprid production was therefore comparatively small. With the exception of 1946 the evidence indicates that failure of the development of the larval population is to a large degree coincident with the failure or irregularities of the diatom population; there is no evidence of any deleterious effect of diatom populations.

THE FACTORS AFFECTING THE LARVAL SEQUENCE

We must now consider the factors which might be responsible for the marked differences which have been found, from year to year, in the development of the larval cirripede population.

(*a*) *A lowered viability of the larval input*

This could arise from either the lowered viability of the parent, particularly during the development of eggs and sperm and at the time of fertilization, or from adverse conditions affecting embryonic development which takes place in the

mantle cavity of the adult. The eggs and sperm are developed during the summer and fertilization takes place during the early winter of the year preceding liberation, embryonic development in the mantle cavity extending therefore from November-December through the winter until the spring months. It is necessary to examine the physical and biological conditions of the environment over this extended period in order to see if there were any abnormalities which might be important in explaining the subsequent behaviour of the population in terms of larval viability. Some climatological data are given in Table 1 (see also Barnes 1955).

Table 1. *Some physical variables for March and April*

Air temperatures 1944-48 from Rothesay records.
Accumulated temperatures are summed day-degrees above 6° C.
Residual wind for 1944-48 from Prestwick records; speeds to nearest 0·1 kn.
The barnacle larval population failed in the years marked with asterisks.

	1944	1945	1946*	1947	1948	1949	1950	1951*	1952*	1954*
Mean temperatures (°C):										
March sea	7·4	6·5	6·4	4·0	7·1	7·2	7·6	6·6	7·3	6·5
March air	—	—	—	—	—	6·3	7·6	4·8	6·6	5·7
April sea	8·3	7·3	7·4	5·3	7·7	8·2	8·2	7·1	7·4	7·5
April air	—	—	—	—	—	8·7	7·6	6·9	7·1	8·4
Accumulative sea temperature	530	402	520	330	460	540	600	482	501	419
Mean salinity (‰) March	—	—	—	—	—	31·05	31·46	32·28	31·91	31·99
Mean salinity (‰) April	—	—	—	—	—	31·52	31·84	32·34	32·55	31·69
Total rainfall (in.) March	1·09	2·95	2·08	4·34	3·51	3·11	2·55	2·97	3·77	3·26
Total rainfall (in.) April	2·69	2·26	1·80	5·36	3·25	5·61	3·33	2·37	2·03	1·93
Residual wind (March):										
Direction (° from N)	280	251	155	118	217	123	204	12	9	5
Speed (knots)	6·5	7·4	3·7	3·3	4·1	0·9	3·3	1·1	2·7	4·1

There is no evidence of any gross departures from the mean values during the nine-year period under consideration, and such small departures as do occur are not correlated with the failure of the larval population to develop. In particular, in the 'failure' years there is no evidence of abnormally high values of either the sea or air temperatures which might be expected to affect adversely the viability of an arctic-boreal species such as *Balanus balanoides*. General observations during the period have not indicated any startling changes or abnormal conditions associated with the failure years.

During most of these years a variety of experimental work has been carried out on other aspects of cirripede biology, both adult and larval. Often hundreds of experiments have been done in a season and in no case has there been any indication of abnormalities in behaviour. No evidence was found for a lowered viability either of the adults during the year preceding liberation or of the larvae at the time of liberation.

(*b*) *An abnormal increase in predation during the larval sequence*

Any real assessment of this possibility in a quantitative fashion is extremely difficult, since it would require a quantitative estimate each year of all the animals likely to feed on the larvae, the collections to be obtained simultaneously with the

larval collections. The animals which might be expected to be most important are the larger plankton organisms such as ctenophores and jelly-fish, possibly the larger copepods and crustacean larvae, *Sagitta*, larval fish and adult plankton-feeding fish. Notes have been made on the zooplankton in the samples each year. During the early spring it largely consists (in addition to the cirripede larvae) of a variety of small copepods and other crustacean larvae together with the cladocerans, *Evadne* and *Podon*, often much *Oikopleura* and frequently numbers of *Sagitta* sp.; fish eggs are often present (see also Marshall 1925). Variations in the abundance of the zooplankton organisms were, of course, encountered from year to year, but in no case were these abnormally great and certainly there was no positive correlation between changes of these zooplankton organisms and the occurrence of the failure of the cirripede population to develop normally; any such correlation would almost certainly have been noted, since the causes of the fluctuations in the cirripede population were very much in mind when the plankton samples were being examined. The evidence on the fish population is less direct; it is rather early for most fish larvae in this area, as is evidenced by the abundance of fish eggs and the lack of fish larvae in the samples. Herring are the only plankton-feeders present at this time, and since they spawn in the area in late February and early March both larvae and adults could be concerned in the predation. Spawning takes place at several localities in the Clyde, notably on the Ballantrae Banks and to a less extent to the south of Arran. That larval herring were responsible for abnormal predation is unlikely, since apart from their absence in the plankton samples the spawning grounds are some forty miles distant and the young herring do not reach the upper parts of the Firth until later (Marshall, Nicholls & Orr 1937, 1939). The only evidence regarding the possible effect of adult herring is such as can be deduced from the landings of spring spawning herrings. The

Table 2. *Landings of main spring herring in the Outer Clyde district*

	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
Total crans	18 633	—	—	135	9 443	14 197	14 935	10 813	9 850	7 362
Total arrivals	1 608	—	—	194	1 695	4 979	2 556	3 262	1 904	2 256
Average catch per arrival	11·6	—	—	0·7	5·6	2·9	5·8	3·3	5·2	3·3

available data are shown in Table 2. There is no evidence of any gross variation in stock over the sampling period and certainly no correlation between landings and the abnormal barnacle years. All the available evidence therefore indicates that predation is not the factor responsible for the sudden depletion of larval cirripedes found during the course of the survey.

(*c*) *The deleterious effect of the physical environment*

Under this heading we include such factors as salinity, rainfall and temperature

during the time the larval population is present in the plankton. Examination of the records does not indicate a large variation from year to year; nor were there any sudden changes at the time when the nauplii virtually disappeared during the 'failure' years.

(*d*) *The presence of deleterious water factors*

By this is understood the presence in the water of substances which are inimical to larval development or the absence of substances necessary for that development. Under this heading are included trace elements and the subtle unknown factors investigated by Wilson (1951) and Wilson & Armstrong (1952, 1954) such as give rise to the different biological properties of water masses and which they have attempted to assess by their effect upon the development of the larvae of *Echinus esculentus*. There is no evidence that such factors are responsible; comparative tests during two recent years made by Wilson between Clyde water and that of the English Channel have shown the former to be as good as or better than the latter. In 1952, for example, Clyde water (which was taken from the centre of the Fairlie Channel) was found by Wilson & Armstrong to yield better cultures of the *Echinus* larvae than did samples of water taken at the same period from two stations in the English Channel. In 1953 the larvae did only slightly better in the Clyde water. It is to be noted that 1952 was a year of cirripede 'failure'. It is also difficult to imagine that any such factor as is being considered by Wilson would arise quite suddenly during one or other stages of larval development—the whole of which takes only four weeks.

There is further indirect evidence on this subject. The eggs of *Echinus esculentus* are used by a large number of visiting workers each year at this station. Inquiries and often close co-operation in this work has at no time indicated a sudden change for the worse in the behaviour of the eggs during this experimental work, and although *Echinus* spawns a month or six weeks later than the cirripedes this work strongly suggests that no major changes have taken place in the biological properties of the local water masses during the past few years.

(*e*) *Defective sampling due to diatoms*

Although the net mesh would let most of the individual frustules of the common diatoms through, in the presence of a large diatom outburst, particularly of *Skeletonema costatum* which forms chains, there is no doubt that clogging takes place, and the fishing capacity of the Indicator is reduced. If the depletion of the larval population were coincident with a large diatom increase then clogging of the net would be immediately suspected as a possible explanation. However, with the exception of 1946 the diatoms were not particularly abundant when the larval population failed. It is clear, therefore, that although this factor may explain Pyefinch's results in 1946 rather than the theory he put forward concerning the deleterious effects of the diatom increase on development of the late stage nauplii, it cannot explain the sequence of events in other years.

(*f*) *Biotic factors associated with a diatom increase*

There has been much discussion and there is still much difference of opinion on the possible effect of dense phytoplankton patches on the behaviour and survival of zooplankton organisms. However, as has been pointed out above, with the exception of 1946, the failure of the cirripede larvae was not coincident with a dense diatom population and any anti-biotic effect of the latter can therefore be ruled out as an explanation of the failure under consideration. It is also worth pointing out that even in 1946 the failure of the cirripede population was not coincident with a sudden diatom increase. The diatoms were present during the early stages of the cirripede larvae and persisted to the later stages. It seems unlikely that anti-biotic effects such as have been envisaged would be specific to the later stages.

(*g*) *The absence of an adequate food supply*

All the larval stages up to the cyprid appear to feed, and an adequate food supply is necessary for normal development. Now an examination of the data shows that deviations from the normal in the development of the larval population are almost always associated with abnormalities in the diatom increase. In the normal seasons (p. 76) the diatom increase was typical: a fairly sudden appearance and rapid development of a high density of *Skeletonema costatum* (Marshall & Orr 1930). In 1951 the outburst of *Skeletonema* did not take place in March but was delayed until May. *Chaetoceros* sp. and *Coscinodiscus* sp. were present in March, but not in great numbers and these diatoms did not give a dense phytoplankton bloom. During the period when late stage nauplii and cyprids would have been expected there were comparatively few diatoms in the water. In 1952 the *Skeletonema* outburst was initiated about the normal time, and there was some development of the larval population. However, quite suddenly *Skeletonema* disappeared, and the late stages and cyprids were relatively few. *Skeletonema* appeared in numbers again late in April coincident with a second outburst of *Balanus balanoides* and this produced a late spatfall. The year 1954 was very similar to 1952: an initial outburst of larvae did not develop and at the same time diatoms were almost completely absent for some weeks. Indeed the clarity of the water and the absence of colour in chlorophyll extracts of net samples was quite abnormal for this time of the year. There was a later diatom outburst and a somewhat protracted production of larvae which gave a long but moderately successful spatfall.

It seems reasonable to conclude that a moderate spring outburst of phytoplankton is necessary, at any rate in this region, for a successful development of the larval population of *B. balanoides*. An exceptionally heavy outburst may be deleterious but there is little evidence that this is the case. The dependence would appear to be a question of an adequate food supply for larval development since most of the stages feed. It is now important to elucidate the factors which determine the variations both in time and intensity of the annual spring diatom outburst.

THE EFFECT OF THE FLUCTUATIONS OF WIND

We have seen that there is no correlation between the failure years and the physical conditions of the immediate environment. However, an examination of the wind data suggests very strongly that the failure years are correlated with this factor. In all the seasons when larval population development was abnormal there was a residual wind component from the north-east quadrant during the month of March, and in those years where we have the most detailed quantitative data (1951, 1952 and 1954) the residual wind was almost due north (Table 1). In 1954, when the diatom outburst was extremely abnormal, the mean residual wind was from 5° and had the high value of 4·1 knots. In the most successful years the residual wind was from the south-westerly quadrant with a high mean velocity or from the south-east with only a moderate resultant.

There has been much work recently on the water exchange in estuaries and it has been shown to have an important controlling effect on the maintenance of populations of sedentary invertebrates with a planktonic larval stage. Conditions in the Firth of Clyde are not analogous to a small estuary, but recent work has shown that the surface currents are closely related to the wind conditions and that changes may be rapid and striking. It is considered that northerly winds contribute to the apparent failure of the barnacle larval populations by driving them in the surface currents into the main body of the Firth with a consequent greater dilution and wider dispersal. From one point of view this effect may be considered an aspect of the sampling problem; the samples even over one and a half miles tow in a restricted part of the Firth were biased. On this view the larval population did not fail; it was merely more widely dispersed. However, such a wider dispersal would in turn tend to give a lower spatfall since the chances of the dispersed individuals reaching suitable intertidal surface for their settlement are greatly reduced. This is in accordance with the fact that occasionally a very sheltered bay may have a successful year when the general settlement has been poor.

It is believed that the direct effect of wind on the sampling and on the wider dispersal of the larvae is a contributory factor to the failure years, but that abnormalities in diatom production have the more important direct action on the larval population. However, the correlation between wind and 'failure' years must also extend to the abnormal diatom seasons since these latter are themselves correlated with the failure years. Evidence is accumulating that wind speed and direction with their profound effect on the currents and on the mixing processes in relation to both vertical and horizontal transfer are of extreme importance in controlling the course of the spring diatom outburst.

THE RELATION TO FLUCTUATIONS IN ADULT STOCK

Variations such as have been described above in the development of the larval population will clearly contribute to fluctuations in the stock of adult barnacles. Where conditions are favourable for the species the output of larvae is so enormous

that such fluctuations are of little importance in the survival of the species, but since adult life over the greater part of the inter-tidal zone is at the most four years, a succession of failure years in a region where the species is existing at or towards the limit of its distribution, could reduce the stock to a dangerously low level for species survival. Such factors may indeed finally delimit the species when the physical factors would of themselves perhaps allow a small but further extension of the distribution. Recently Southward & Crisp (1954, 1956) have considered long-term trends and short-term fluctuations in the relative quantities of *B. balanoides* and *Chthamalus stellatus* (Poli) at a number of places in the British Isles. They consider that the major changes can be correlated with long-term temperature trends, and that in some areas annual temperature changes affect the relative numbers and distribution in a significant fashion. It would seem that some of these fluctuations may in part be explained as the result of the factors discussed above acting together with or even over-riding any temperature effects. When the two species are in competition over any part of the shore, failure of the *Balanus* spatfall will allow the gap to be filled by *Chthamalus*. The factors discussed above will not act on *Chthamalus* and *Balanus* alike since the former breeds during the summer months; indeed failure of the spring *Balanus* settlement is ideally suited to the spread during the same year of *Chthamalus* in the summer months (Barnes 1956).

Table 3. *Frequency—direction of monthly residual winds, 1901-49*

Direction	March	April	July	August
0-90°	4	9	4	4
91-180°	17	9	6	6
181-270°	21	20	33	32
271-360°	7	11	6	7

That fluctuations result from causes other than temperature changes is suggested by the difference between embayed situations and the nearby more open coast, (Southward & Crisp 1954, 1956, Hatton & Fischer-Piette 1932) and, as noted above in the Clyde. That larval dispersal under the influence of wind driven currents will show considerable variation from year to year in the south-west is indicated by the data of Dietrich *et al.* (1952) for the mean residual monthly wind speeds and directions for the years 1901-49 in the western English Channel. The frequency distribution of the wind direction has been computed from this data for two spring months and two summer months (Table 3). In March particularly there is a wide spread in the frequency indicating considerable yearly variations; the same tendency is evident in April although in a different sense, the general shift being towards the northerly direction. Both months stand in marked contrast to the very sharply defined maximum frequencies from the south-west during the two summer months. In addition to failure of the larval population Barnes & Powell (1950) have pointed out how a very heavy settlement can be self-eliminating and reduce the stock with a tendency for the few subsequent years to be poor.

The effect of physical conditions influencing larval dispersal and the presence or absence of an adequate diatom population should therefore almost certainly be added to temperature fluctuations as factors regulating the dynamic equilibrium between the two species.

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SUMMARY

1. An account is given of variations in the development of the larval population of the common shore barnacle *Balanus balanoides*; results extending over ten years are reviewed.

2. The normal sequence is for liberation of nauplius I in March, development through the several naupliar stages to cyprids and settlement in early April.

3. In some seasons, the 'failure' years, liberation and development of early stage nauplii is followed by a more or less catastrophic reduction in numbers of cyprids.

4. The possible causes for this failure are examined; neither lowered viability of the larval input, an increase in the predation, the deleterious effect of the physical environment, the presence of deleterious water factors, defective sampling due to diatoms, nor biotic factors associated with a diatom increase appear to be the causative factor.

5. 'Failure' years are associated with abnormalities in the spring diatom outburst, which it is suggested is an important controlling factor, acting through its nutrient value to the developing larvae.

6. Winds appear to be correlated with the failure years; this could be regarded as a sampling effect, but in addition could be the primary cause of diatom variations.

7. The effect of such fluctuations on the parent stock is considered.

8. The importance of the results to any consideration of fluctuations in the relative proportion of *Balanus balanoides* and *Chthamalus stellatus* is considered.

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AERIAL DISPERSAL IN A KNOWN SPIDER POPULATION

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(With 9 Figures in the Text)

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SPECIES, NUMBERS AND ACTIVITY PATTERNS

(*a*) *Introduction*

Although it has been known since the time of Aristotle that spiders can make airborne excursions, the first accurate observations were published by the pioneer British arachnologist, John Blackwall (1827). It was not until some years later that McCook (1877, 1878, 1889-93) made the suggestion that such behaviour might be a means of dispersal for the species concerned and during the last fifty years a number of arachnologists have published observations on this subject (Nielsen 1932, Braendegaard 1937, 1938, 1946, Bristowe 1929, 1939, Berland 1932, Smith 1904, Emerton 1908, 1919, McKeown 1952). In addition to the work of these observers, the contribution made by spiders to aerial plankton has been demonstrated by collections from aircraft towing nets (Collins & Baker 1934, Crosby & Bishop 1936, Glick 1939) and from nets on wireless masts (Freeman 1946) and the masts of ships (Hardy & Milne 1937). Generally speaking only small numbers were taken, though Glick was able to collect about 1500 specimens, including 4 at 5000 ft. Freeman used three nets 1 yd in diameter, and during 1934 and from March to April 1935 he took 134 specimens, representing twenty species. On the other hand, Owen & Le Gros (1954) found that seventy meals taken by swifts in July and August 1952, July 1953 and July 1944 contained 1425 spiders, representing about twenty-two species. Bristowe (1939) gives an excellent account of dispersal behaviour and summarizes much of the published work. The following general points emerge:

1. Aerial dispersal is recorded for a great many species of spiders in boreal and temperate Europe and also other parts of the world.

2. This type of dispersal may occur any time of the year either by immature or adult spiders, and is divisible into two categories: (*a*) The dispersal of the juveniles chiefly during the summer months, in which many families are represented. (*b*) The dispersal, mainly during the autumn, winter and spring, of members of the family Linyphiidae, when the majority of the individual spiders are adult.

3. Mass dispersals (forming the bulk of the literature on the subject) are known only for 2 (*b*) and usually take place on calm, sunny days in the cold seasons of the year.

The autumn, winter and spring dispersals of adult Linyphiidae have most often attracted the attention of biologists, not only because it may be a striking phenomenon to witness and related in nearly every case to particular weather conditions, but because the factors stimulating this activity have not been clear. The dispersal of young spiders soon after hatching is more easy to understand because of the local formation of dense populations and the cannibalistic tendencies of the individuals, and the process is generally continuous throughout the summer, taking place in different weather conditions, though it is not usually characterized by the sudden appearance of very large numbers of spiders. The linyphiid dispersal on the other hand is especially evident during the winter months, consisting mainly of the adults of both sexes and the bulk of the individuals taking part (in this country at least) are members of a small number of species. Few attempts to explain the behaviour have so far been advanced. Bristowe (1939) has suggested that the rapid rise in temperature on a sunny day after a cold night causes discomfort to spiders which have been conditioned to the cold, and that they are stimulated to move away. Nielsen (1932), who states that October is the chief time of the year for mass migration in Denmark, believed that as a warm sunny morning after a frosty night first causes the ground to become very wet, the resultant high humidity is disliked by the spiders which emerge for dispersal when the ground begins to dry out.

During 1951-52, while studying the spider population of a small area (5½ acres) of limestone grassland on the Wytham estate of Oxford University, the opportunity was taken to record aeronautic activity. By various sampling methods, to be described in another paper, the species composition of the area was known fairly accurately, and some estimate could be made of the population density. It was therefore possible to say which species in this particular community took part in aerial dispersal, at which stage in their life history, and to relate this activity to population density. At the same time, a number of temperatures were taken in and on the vegetation of the experimental area, and these in conjunction with standard meteorological data could be related to the dispersal behaviour.

(*b*) *Study area and methods*

The Wytham estate includes about a thousand acres of mixed deciduous wood-

land on a coral rag limestone outlier, six miles north-west of Oxford, in Berkshire. An enclave on the southern slopes of this wood extending over about $5\frac{1}{2}$ acres is divisible into three types of ground vegetation: limestone with practically no soil and a thin vegetation covering, a luxuriant turf mainly *Festuca rubra*, and a nearly pure sward of *Brachypodium pinnatum*. Although adjacent, each vegetation type had a distinctive spider population and each was sampled separately. Over a period of fifteen months, four quadrats of turf (25×25 cm) were taken at random in each area between two and four times a month, a series of thirty-four pitfall traps was laid down, and frequent hand collections were made.

In January 1951 on a mild but overcast day a number of small linyphiid spiders were noticed climbing up the stems of dead *Pastinaca sativa* plants, and as they reached the flower head the abdomen would be raised, a strand of silk extruded, the spider became air-borne and drifted away. In this case, an energetic dispersal was taking place under conditions of 10/10ths cloud, but the weather was unusually mild. Other instances of linyphiid dispersal in the spring of that year were recorded, but not on the same scale as in January.

In August 1951 an attempt was made to catch dispersing spiders by placing out a number of 4 ft canes in the turf area on which a band of greasy 'fly paper' had been fixed about half way up. The grease bands did not retain their stickiness very long, however, and were soon replaced by a resinous compound used to 'band' fruit trees. This material with the proprietary name of 'Sticktite' was smeared round the cane, forming a band about 10 in. deep. It was found to be perfectly satisfactory for this purpose, though inclined to be too runny in hot weather and rather congealed in cold.

Not all spiders caught in this way can be called aeronauts. At certain times of the year, particularly in the autumn, there is a considerable amount of wandering about by those species which normally spin their webs on the herb layer plants, e.g. the young of *Theridion sisyphium* and *T. impressum* and by hunting spiders such as some Lycosidae, Thomisidae, Salticidae and Clubionidae which will climb up tall plants and canes quite readily. Some elimination is therefore often necessary when listing species caught during dispersal behaviour though it is quite likely that some of the members of the families mentioned above may have been about to disperse, particularly if they were juveniles. Nielsen (1932) mentions that in Denmark, whenever floating threads of silk were caught, immature crab-spiders (Thomisidae) were almost always to be found suspended from them. In Wytham, this family was not recorded as playing any great part in dispersal movements.

On 28 August 1951 thirteen greased canes were put out in the *Festuca rubra* habitat and nine in the *Brachypodium pinnatum*. Collections were made from them from time to time during September, October and November, but very small numbers of spiders were caught. These catches are regarded as unsatisfactory because the sticky bands were often very quickly smothered with winged insects, particularly midges, and became ineffective as traps. In addition it was not possible to visit them often enough. The flower heads of the numerous dead *Pastinaca sativa* plants were also examined particularly during October 1951 and collections

made of spiders which appeared to be dispersing. On 4 December all of the canes in the *Festuca* habitat (B) were replaced by twelve freshly greased canes and those in the *Brachypodium* (A) replaced by six. On 14 December six greased canes were put out in area C (limestone with thin vegetation covering) and five placed a few yards inside the wood to the north of the study area. The collections from the latter contrasted in a very interesting way with the catches from the other canes.

This final arrangement (Fig. 1) was maintained until 14 May 1952 when the

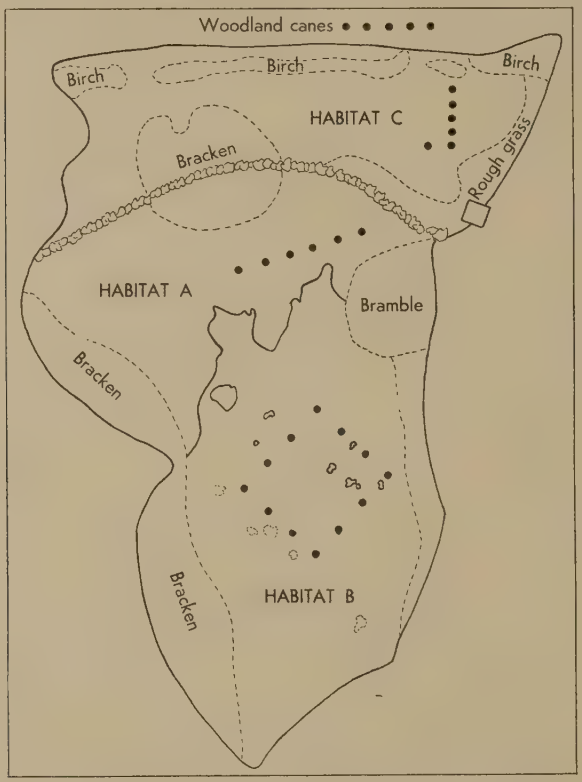

Fig. 1. The distribution of canes in the study area.

last collection was made. During this period, December to May, the canes were visited twice a month or more frequently, the catch taken and fresh grease put on. After the middle of May the technique became ineffective because of the large numbers of winged insects which were caught.

(*c*) *Species composition, seasonal change and sex ratios*

In the following account the monthly catch from the thirty-four pitfall traps which gives some measure of the duration and intensity of horizontal movement, is referred to as *ground activity*. The term *aeronautic activity* is used to describe the

duration and intensity of aerial dispersal as estimated by the monthly catch on the twenty-four canes. Population density is estimated from the mean of the number of spiders taken from the quadrat samples obtained each month.

In Table 1 the catching period has been arbitrarily divided into three: from 28 August 1951 to 7 January 1952, during which time most of the specimens

Table 1. *Aeronauts taken in grassland from August 1951 to May 1952 in order of abundance*

28 August to 7 January*	Number	%
Tapinocyba praecox	38	26·5
Erigone dentipalpis	26	18·8
E. atra	10	7·0
Bathyphantes gracilis	9	6·2
Meioneta rurestris	9	6·2
Lepthyphantes tenuis	6	4·1
Araeoncus humilis	5	3·4
Savignia frontata	4	2·8
Lepthyphantes mengei	1	0·7
Centromerus sylvaticus	1	0·7
Centromerita bicolor	1	0·7
Unidentified (immature)	33	23·0
Total	143	
Adults		77
8 January to 26 February		
Savignia frontata	30	23·6
Tapinocyba praecox	20	15·7
Erigone atra	19	14·9
Bathyphantes gracilis	9	7·0
Erigone dentipalpis	7	5·5
Meioneta rurestris	4	3·1
Araeoncus humilis	4	3·1
Pachygnatha degeeri	2	1·5
Meioneta mollis	1	0·7
Lepthyphantes tenuis	1	0·7
Unidentified (immature)	30	23·6
Total	127	
Adults		76·4

27 February to 14 May	Number	%
Savignia frontata	95	23·0
Theridion pallens	30	7·2
Meioneta mollis	25	6·0
Cnephalocotes obscurus	24	5·8
Bathyphantes gracilis	22	5·3
Erigone atra	21	5·0
Meioneta rurestris	13	3·1
Araeoncus humilis	13	3·1
Pachygnatha degeeri	10	2·4
Tapinocyba praecox	9	2·1
Lepthyphantes tenuis	6	1·4
Erigone dentipalpis	6	1·4
Wideria arctica	3	0·7
Oedothorax agrestis	1	0·2
Micrargus herbigradus	1	0·2
Oedothorax apicatus	1	0·2
Tiso vagans	1	0·2
Dismodicus bifrons	1	0·2
Unidentified (immature)	141	34·1
Total	413	
Adults		65·9

* Mainly October and December

collected were taken by hand in October and December; 7 January to 26 February and 27 February to 14 May 1952, when the collections were made entirely from greased canes. Inspection of the species lists and the numbers of specimens taken clearly shows that the commonest species have well-defined periods of aeronautic activity.

Tapinocyba praecox, which has not previously been recorded as taking part in aerial dispersal, was a common spider in the study area and formed the largest percentage of the catch in autumn and early winter. In January and February it gave way to *Savignia frontata* and declined rapidly during the spring months. *Erigone atra* and *E. dentipalpis* are probably the two best known British aeronautic spiders and usually form the bulk of recorded collections. Unfortunately these two spiders are not separated in the largest collection which has been made (Smith 1904) when they formed 43% of over 5000 aeronautic spiders taken

in October and November 1903. Bristowe (1939) lists collections of these two species made during October, November and December in different years and at different places, and *E. dentipalpis* outnumbers *E. atra* by 169 to 78. For the same season my catches showed a similar trend (Table 1): 26 *E. dentipalpis* to 10 *E. atra*. A hand collection of aeronauts from 16 to 29 October produced 15 *E. dentipalpis* to 4 *E. atra*. From January to May, however, the numbers are reversed, *E. atra* outnumbers *E. dentipalpis* by over 3 : 1. On 3 March 1954 in Norfolk a hand collection produced 23 *E. atra* and 2 *E. dentipalpis*.

The catches made from 7 January to 26 February and from 27 February to 4 May cover roughly equal periods, forty-nine and forty-seven days respectively, and in each case the catch was taken from twenty-four canes. The latter period produced 413 specimens of eighteen different species, while the forty-nine days in January and February produced 127 spiders representing ten species. This seems to show that with the coming of warmer weather in the spring a larger number of individuals and species are able to disperse, quite apart from other factors, which may be influencing this behaviour. Bristowe (1939) states that the sex ratio in his collections was 417 males : 410 females, while Emerton in America found that he had taken many more males than females. In both cases the collections are from different places and on different dates, so that the true state of affairs is probably obscured. The Wytham collections for the three periods discussed above show that females are considerably more numerous than males,

Table 2. *Sex distribution in Wytham collections*

	Males (%)	Females (%)	Total adults
28 August 1951—7 January 1952	24·5	75·5	110
8 January—26 February 1952	19·5	80·5	97
27 February—14 May 1952	33·4	66·6	272

though this may not hold for every species (Table 2). In the latter period (February to May) numbers of *Theridion pallens* appeared in the catches and twice as many males as females were caught (twenty males to ten females). This occurrence has contributed to the lower proportion of females in Table 2. This species is typically an arboreal spider occurring most commonly on tree and bush foliage. During the period 16 April to 14 May five canes in the wood caught 44 *T. pallens*, while for the same period twenty-four canes in the adjacent grassland caught only 30. If the number of canes in each habitat had been the same, the expected catch in the woodland would have been something like seven times as great as that in the grassland.

In all, the total of adult *T. pallens* taken was seventy-four of which 82·4% were males. It is possible, however, that if the catching had been continued after 14 May, when the numbers were increasing, the sex ratio might have been different. There were many cases in Wytham to show that the male season of maturity was often characterized by a short burst of activity while the female has generally

a more extended season. This has been convincingly demonstrated by Tretzel (1954). Table 3 lists eight common grassland aeronauts and the numbers of males

Table 3. *The numbers of eight common grassland aeronauts taken on the canes from 14 December 1951 to 14 May 1952*

	Males	Females	
	(no.)	(no.)	(%)
Tapinocyba praecox	4	72	94·6
Savignia frontata	43	97	69·2
Erigone dentipalpis	8	12	60·0
E. atra	13	33	71·7
Meioneta rurestris	6	12	66·6
M. mollis	14	16	53·3
Cnephalocotes obscurus	10	14	58·3
Bathyphantes gracilis	8	29	78·3

and females taken on the canes from 14 December 1951 to 14 May 1952. It seems likely that the relative numbers of males and females which disperse by aerial means varies from species to species, but although in four out of the eight in Table 3 the figures are rather low, in general the sex ratio is clearly biased in favour of the females. In the case of *Meioneta mollis* and *Cnephalocotes obscurus* the sexes are present in nearly equal numbers but comparatively few specimens were taken.

Tapinocyba praecox is of special interest as an aeronaut because it was a very numerous spider in the grass turf. The figures in Table 3 show that 94% of the specimens taken on the canes were females, and those in Table 1 show that in autumn and early winter this species makes up the largest proportion of aeronauts. The proportion falls during January and February and there was a considerable drop in the period March to May. If we compare this with the data in Fig. 2 it can be seen that the highest densities of females occurred during the period September to January. There was then a gradual fall until the lowest figures were recorded in July and August. In this species, therefore, the most intense aeronautic activity took place when the population density in the grass was at its highest, though the numbers on the canes fell off more rapidly during the spring than did the numbers taken in the turf samples (Table 4). Fig. 2 shows also that the male season takes a form very different from that of the female. During mid- and late summer few adult males were taken, but in September they suddenly appear in large numbers and the catch for this month with October was slightly higher than the catch taken in all the other months put together (86·6 : 85·8). The only males trapped on the canes (four) were taken in the period 4 to 14 December 1951. Although several hand collections were made and small catches taken from the first set of greased canes, the period of male abundance (September and October) was not covered by an efficient trapping technique. Nevertheless, if the males had been as active as the females one could not have failed to detect them.

Throughout the twelve months' period referred to, twenty pitfall traps (1 lb

jam jars) were laid out in the *Tapinocyba praecox* habitat, and although few specimens of this species were caught, it is of interest to note that of the eleven specimens taken eight were males. This slight evidence suggests that the male may be capable of some horizontal activity, presumably when searching for a mate, but does not normally disperse by aerial means. On the other hand, activity in the female is mainly a vertical dispersal movement. Although only eight males were taken in the pitfall traps, none was taken in the period September to December, when the population density was at its highest. They occurred as follows: two each in January and February, three in March and one in April.

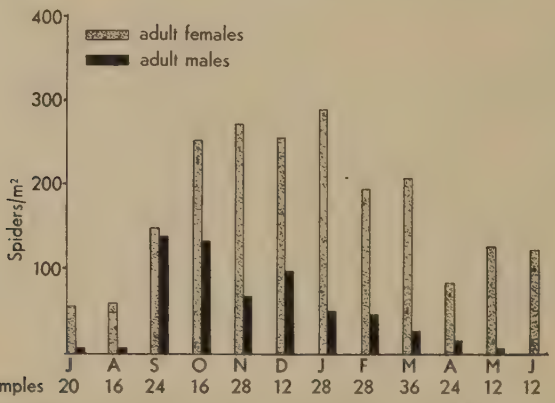

Fig. 2. The population density of *Tapinocyba praecox* in habitats A and B estimated from quadrats (25 × 25 cm) of turf, of which the numbers shown were taken each month.

The Wytham cane catches showed *Erigone atra* to be less numerous than *E. dentipalpis* in the autumn and early winter, and more numerous from January to May. Most of the specimens of these two species, which are two of the commonest British aeronauts, were taken in area C. In Table 4 the numbers of these two species caught in pitfall traps, quadrat samples and on greased canes per month are shown. The quadrat samples for both species produced too few specimens for one to derive information on seasonal activity and maturity. The same may be said for the pitfall catches of *Erigone atra*, but the same catching technique clearly shows *E. dentipalpis* to be particularly active during January, February and March, with a well-defined peak in February. The small cane catches of *E. dentipalpis* taken from December to April indicate that the female is mainly concerned with this activity in contrast to the predominance of males in the pitfall catch. Aerial dispersal in *E. atra* is recorded for each month from December to May but it has a peak period of aeronautic activity in February and March, while there is no evidence of corresponding activity on the ground. These two closely related species have a marked ecological overlap in many ways, occurring in the same places, with similar periods of maturity, and building similar webs. How they differ biologically is not clear, but these data suggest that there might be important behavioural differences. Knülle (1952, 1953) found *E. atra* common in damp

Table 4. *Monthly quadrat, pitfall and cane catches and sex ratios*

Quadrat figures show density in spiders/m². Except for *Tapinocyba praecox*, for which twenty traps were used, pitfall figures show the catches from thirty-four traps. To catch aeronauts twenty-four canes were used.

Quadrat samples	Jan. 20	Feb. 28	Mar. 36	Apr. 24	May 12	June 12	July 20	Aug. 16	Sept. 24	Oct. 12	Nov. 20	Dec. 8	Sex ratio (♂:♀)
Tapinocyba praecox													
Quadrats	337[1]	240	233	97	132	121	60	64	288	384[4]	339	352[5]	196 : 728
Pitfalls	3	3	3	2	0	0	0	0	0	0	0	0	8 : 3
Canes	3	19	12	4	0[2]	—[3]	—	—	—	—	—[3]	38	4 : 72
Erigone atra													
Quadrats[6]	0	1	1	0	0	1	1	0	1	1	1	0	1 : 6
Pitfalls	0	1	2	1	0	0	4	0	0	0	0	3	6 : 5
Canes	3	14	14	5	1[2]	—	—	—	—	—	—	4	14 : 27
Erigone dentipalpis													
Quadrats[6]	1	1	1	1	0	0	0	0	0	4	3	0	5 : 6
Pitfalls	11	28	11	4	0	0	4	4	2	3		4	55 : 116
Canes	0	7	3	1	0[2]	—	—	—	—	—	—	5	5 : 11
Cnephalocotes obscurus													
Quadrats	10·6	11·2	30·4	7·3	4·3	0	6·4	24	26·4	75·6	20	24	43 : 43
Pitfalls	0	0	1	42	8	10	10	11	1	0	0	0	64 : 19
Canes	0	0	8	16	0[2]	—		—	—	—	—	0	10 : 14
Savignia frontata													
Quadrats	44·8	13·6	7·0	0	0	0	0	0	5·2	32	32	8.0	16 : 28
Pitfalls	1	1	0	0	0	0	0	0	0	0	0	0	—
Canes	0	41	49	16	1[2]	—	—	—	—	—	—	0	29 : 78
Meioneta mollis													
Quadrats	12·8	6·8	5·2	2·5	0	0	0	0	10·5	10·5	25·6	8·0	10 : 14
Pitfalls	0	0	0	0	0	1	0	2	1	0	0	0	—
Canes	0	1	15	0	0[2]	—	—	—	—	—	—	0	9 : 17
Meioneta rurestris													
Quadrats	—	—	—	—	—	—	—	—	—	—	—	—	4 : 3
Pitfalls	0	0	1	0	0	0	2	16	2	0	0	2	13 : 10
Canes	0	5	5	7	0[2]	—	—	—	—	—	—	2	6 : 13
Bathyphantes gracilis													
Quadrats	—	—	—	—	—	—	—	—	—	10		—	3 : 8
Pitfalls	2	3	0	0	0	7	12	20	21			7	15 : 67
Canes	0	9	11	9	1[2]	—	—	—	—	—	—	7	8 : 29
Lepthyphantes tenuis													
Quadrats	—	—	—	—	—	—	—	—	—	13		—	1 : 6
Pitfalls	2	4	4	3	1	5	13	19	19			9	19 : 73
Canes	0	1	4	1	1[2]	—	—	—	—	—	—	3	4 : 6

[1] 28 samples. [2] First half-month only. [3] *Tapinocyba praecox* was the commonest aeronaut in hand catches especially in October and November.
[4] 16 samples. [5] 12 samples. [6] The number of samples varied from month to month averaging 20. No correction has been made to the figures because the numbers were too small.

places along river banks and on certain parts of the coast. *E. dentipalpis* was apparently much less common and is described as tolerating a wider range of conditions. The short period of intense ground activity shown by *E. dentipalpis* and several other species, appears to be an indicator of mating behaviour, as far more males than females are caught. On reaching maturity the male of many species is known to become very active during the search for a mate. *E. atra* and three other common aeronauts have shown little or no evidence of this sort of activity, so that mating behaviour may take a different form.

In the Wytham study area, both species were scarce in the *Festuca rubra* and *Brachypodium pinnatum* habitats, but were quite common in habitat C where, however, there appeared to be a considerable difference in their relative numbers. Collections of spiders from small sheet webs in this habitat taken at random produced the following numbers of adults of these two species: *Erigone dentipalpis*, 1 male and 19 females on 11 March 1952, 2 males and 5 females on 4-5 October 1951; *E. atra*, 1 male and 2 females on 11 March 1952, 1 male on 4-5 October 1951. No immature specimens were taken during March, but the October collections included twenty-two immature spiders, some of which may have been of these two species. Although *E. dentipalpis* appears to be the commoner spider in this locality *E. atra* is the more vigorous aeronaut in the early months of the year.

Tretzel (1954) used pitfall traps in the Erlangen area of Germany on a fairly extensive scale and took the following numbers of *E. atra* and *E. dentipalpis* respectively: 152 males, 21 females, 59 males and 27 females. He found that the catches of *E. atra* showed a peak extending over May, June and July, and similarly May and June for *E. dentipalpis*. His traps were distributed over a wide range of habitats which were apparently much more favourable to *E. atra*. The Wytham pitfall catch of this species amounted to only eleven specimens in a twelve-month period with the highest total (four) in July. In contrast *E. dentipalpis* was the commoner of the two species in Wytham and the activity peak is in February as opposed to May and June in the German locality.

The population density of *Cnephalocotes obscurus* shows two peaks, in March and October, but the period of maximum ground activity begins with a sharp rise in April as the quadrat population is declining, and is extended at a lower level throughout the summer months when the population density is at its lowest. The double peak is shown by both males and females. The onset of maximum activity on the ground when the male is most active is coincident with the aeronautic catch which is sharply confined to March and April. These aspects of the behaviour are in contrast to *Tapinocyba praecox*, whose aeronautic activity took place during the period of maximum population density. In addition both male and female of *Cnephalocotes* were aeronautic, while in *Tapinocyba* this activity was confined almost entirely to the latter sex. *Cnephalocotes obscurus* also has an extended period of maturity for both sexes covering ten to eleven months of the year, and the sex ratio at any given time appears to have been roughly 50 : 50. Tretzel (1954) took thirty-four males and twelve females of this species during three years' pitfall

trapping at Erlangen, Germany, and records a minor peak in both May and October, but no catch is recorded for July, August and September. No specimens appeared in Wytham traps from October to February inclusive.

Savignia frontata follows a similar pattern to *Cnephalocotes obscurus* in that the grass samples showed it to be mature during the colder months of the year, and that mature males were taken in as many months as mature females. The figures give the impression that there may be two population peaks, but the small December figure may be due to inadequate sampling. If this is so, then the numbers began to build up in September, reached a peak in January and declined again in March. As in the case of *Erigone atra*, there was a vigorous aeronautic dispersal but practically no ground movement, so that only two specimens are recorded from pitfall traps. The development of aeronautic activity follows on a month or more after the peak has been reached in population density, but it is likely that this time difference varies according to the weather conditions. Aerial dispersal may be delayed some weeks if conditions are unfavourable, a subject to be discussed later.

Although relatively few specimens of *Meioneta rurestris* and *M. mollis* were taken, there is coincidence in the population peaks derived from the three collecting methods. The quadrat catches show that *M. mollis* has a well-defined population peak in November; the largest monthly catch of *M. rurestris* was also taken during this month, though some specimens were caught in October, December and February. In both cases, the pitfall traps took all or nearly all their catches in August and September, and the main aeronautic activity was in the spring from February to April. The separation of the three peaks in time seems to be well established. The female is again the more active aeronaut, but ground activity in *M. rurestris* seems to be almost equally shared by both sexes. Tretzel records mature *M. rurestris* males in his pitfall traps during June and July and mature females in May, June, July, September and October. There was no catch in August, the month which produced the largest numbers in Wytham.

Bathyphantes gracilis follows *Meioneta rurestris* closely in activity pattern and in appearing in the quadrat samples only from September to February with the highest total in November, but the catch was small. Both have a ground activity peak from July to September and a dispersal peak in the spring from February to April, though in each case the December aeronautic catch suggests that this form of activity commenced fairly early in the winter but was inhibited during the unfavourable weather of January 1952. *Bathyphantes gracilis* and *Lepthyphantes tenuis* are both remarkable in that the pitfall traps caught a much higher proportion of females than males. It has been postulated (Tretzel 1954) that the peak period of ground activity is an indicator of the mating season but although this has been clearly established in many species from several families, it cannot be applied in the same way to *Lepthyphantes tenuis* and *Bathyphantes gracilis*. The females of both species construct small sheet webs low in the vegetation and as males have been taken on them, presumably during courtship behaviour, there is no evidence that the female leaves her web to hunt for a mate. It is usual in web-spinning spiders for the mate to contact the female at her web and for mating to

take place there. A purely hypothetical explanation put forward here is based on the observation that very often in late summer many of the presumed webs of *Lepthyphantes tenuis* have been found to be unoccupied. It is possible that when the female of this species and *Bathyphantes gracilis* are sexually mature they build a larger number of webs in different places, remaining with each one only a short time if a male does not turn up. During this increased activity they are caught in the pitfall traps and in fact have very often been observed to construct their webs in them. I am indebted to Edwin Nörgaard and G. H. Locket for the suggestion that the higher catch of females may be due to increased activity during the egg-laying period when searching for a suitable site to deposit the egg cocoon. Tretzel (1954) also records certain linyphiid species from his traps in which females outnumber males, e.g. *Stylothorax retusa* and *Lepthyphantes tenebricola*, or in which

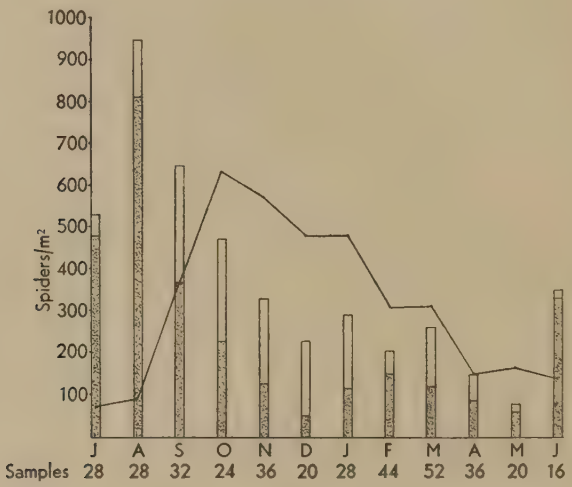

Fig. 3. The population densities of immature and juvenile (stippled) linyphiid spiders from quadrat samples. The curve shows the density of adults of the twelve most numerous of the linyphiids inhabiting 'litter'.

there were only small differences between the numbers of each sex caught, but no explanation is attempted.

The nine linyphiid spiders which are discussed in detail in this section were characterized by a considerable variation in their activity patterns though seasonal peaks were usually well-marked. With two exceptions males predominated in the pitfall catch while the reverse was true for the aeronautic catch.

Table 4, which presents estimates of population density for nine different species of aeronauts can only refer to mature specimens because the identity of most immature linyphiids cannot be accurately determined. In Fig. 3 the monthly figures from the quadrat samples of unidentified linyphiid spiders are presented. Superimposed on the histogram is a graph illustrating the monthly population of the

adults of the twelve most numerous linyphiid species typically found in the 'litter' or low down in the herb layer. In spring and early summer, the numbers of both immature and adult linyphiids were low, and the smallest total was recorded for May. In June there is a substantial rise in the numbers of immature spiders and this increases rapidly to the peak in August. The corresponding peak of adult spiders occurs in October, and the lowest point on the curve is reached in July.

Table 5. *Immature spiders in the monthly catches*

	January	February	March	April	May	December
Immature (% of total)	0	26	26·6	38·7	30·7	11·9
Total aeronauts	5	138	210	147	52	67

In Fig. 3 the numbers of the very young or juvenile spiders have been separated from the rest of the immature catch. It can be seen that during June, July and August, when the numbers are rapidly building up to a peak, the bulk of the immature spiders are juveniles, but as the population density falls, this category forms a declining proportion of the total number of immature specimens. There is a second and very much smaller peak in February of juveniles but it does not appear to be reflected in a higher total number of immature spiders.

No reliable figures were obtained for estimating the aeronautic activity of the Wytham spider population from June to November. The published records of this behaviour refer in most cases to late autumn and early winter months, with particular mention of October. It may be significant that the population density

Table 6. *Species list of spiders taken on greased canes, excluding the woodland canes*

Araeoncus humilis (Blackwall)
**Araneus* (*redii*) (Scopoli)
**A.* (*diadematus*) (Clerck)
**A.* (*cucurbitinus*) (Clerck)
Bathyphantes gracilis (Blackwall)
Micrargus herbigradus (Blackwall)
Centromerus sylvaticus (Blackwall)
Centromerita concinna (Thorell)
**Cheiracanthium* sp.
Cnephalocotes obscurus (Blackwall)
*(*Cryphoeca silvicola*) (C. L. Koch)
**Cyclosa* (*conica*) (Pallas)
**Dictyna* (*arundinacea*) (Linnaeus)
**Dismodicus bifrons* (Blackwall)
(*Enoplognatha thoracica*) (Hahn)
Erigone atra (Blackwall)
E. dentipalpis (Wider)
**Heliophanus* (*flavipes*) C. L. Koch
Lepthyphantes mengei Kulczynski
L. tenuis (Blackwall)
**Linyphia peltata* Wider
**Lycosa* (*amentata*) (Clerck)
**Lycosa* (*lububris*) (Walckenaer)
**L.* (*monticola*) (Clerck)
**L.* (*pullata*) (Clerck)
Meioneta mollis (O.P.-Cambridge)
M. rurestris (C. L. Koch)
**Meta* (*segmentata*) (Clerck)
Oedothorax agrestis (Blackwall)
O. apicatus (Blackwall)
O. fuscus (Blackwall)
Pachygnatha degeeri (Sundevall)
**Philodromus* (*aureolus*) (Clerck)
Savignia frontata (Blackwall)
**Singa pygmaea* (Sundevall)
Tapinocyba praecox (O.P.-Cambridge)
**Tetragnatha* sp.
Theridion pallens Blackwall
**T.* (*sisyphium* or *impressum*)
**T. ovatum* (Clerck)
**Theridion* sp.
Tiso vagans (Blackwall)
Widerja antica (Wider)
**Xysticus* (*cristatus*) (Clerck)

* Presumed to be non-aeronauts.
Parentheses indicate uncertain identity or an immature specimen.
Nomenclature after Locket & Millidge (1953).

in the grass of linyphiid spiders during this month is higher than at any other time. As the cane catches did not cover the period June to November, the proportions of aeronauts which were immature is not known. However, young spiders did disperse

aerially in large numbers, and Table 5 shows the proportions of the monthly catches, from 4 December to 14 May which were immature. The young of non-aeronauts, where identifiable, are excluded.

(d) The non-aeronautic component of the spider population

In Table 6 forty-four species of spiders are listed for the cane catches. Of these twenty-two are species which build their webs on field layer plants (therefore also on the canes) or may be expected to climb up plant stems when hunting. Some may have been in the process of dispersing by air, but in the circumstances it is safer to eliminate them from the list of aeronauts. Twenty of the twenty-two aeronauts are linyphiids and most of the common aeronautic species recorded in the literature are included. These twenty Linyphiidae can be classified

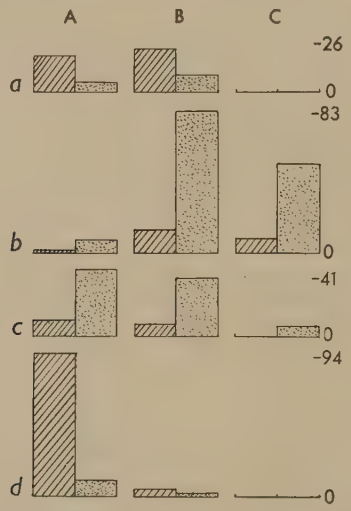

Fig. 4. The catches over a twelve-month period of four common non-aeronautic linyphiids from 364 quadrat samples (shaded) and ten pitfall traps (stippled) in each of the three grassland habitats A, B and C (Fig. 1): *a, Ceratinella brevis; b, Centromerita concinna; c, Centromerus sylvaticus; d, Lepthyphantes ericaeus.*

ecologically as living typically in the 'litter' stratum, or low down in the herb layer. During the period of study, a total of forty linyphiid species was recorded in this area of Wytham grassland, which can be grouped in this way, but of the twenty not recorded in the cane catches, few occurred in large numbers.

Four species of the twenty non-aeronautic linyphiids are worth special mention: *Ceratinella brevis*, *Lepthyphantes ericaeus*, *Centromerus sylvaticus* and *Centromerita concinna*. The last two species were recorded in the cane catches by only one specimen each, and Bristowe (1939) also mentions the occurrence of *Centromerita concinna* in his list of aeronauts. Nielsen (1932) records the capture of two specimens of *Centromerus sylvaticus* in a total of sixty-four aeronauts taken in Denmark during October. As far as is known neither *Ceratinella brevis* nor *Lepthyphantes ericaeus* have been observed to disperse by air in this country. Fig. 4 illustrates

the proportion of these four species taken from grass samples and pitfall traps in the three grassland habitats during a twelve-month period. In each case the greatest amount of ground activity (indicated by numbers trapped) occurs in the area with the highest population density while there is a clear habitat preference shown by all four species. For present purposes it is sufficient to note that *C. concinna* and *C. sylvaticus* which show the greatest amount of ground activity in relation to population density are known to disperse by air but this behaviour appears to be very weakly developed. Although present in considerable numbers in the *Brachypodium*, *Lepthyphantes ericaeus* moves about very little on the ground when mature and has not been recorded as an aeronaut.

A further fifteen species (from other families) in the total recorded spider fauna were found living in this stratum and only two were taken in the aeronautic catch:

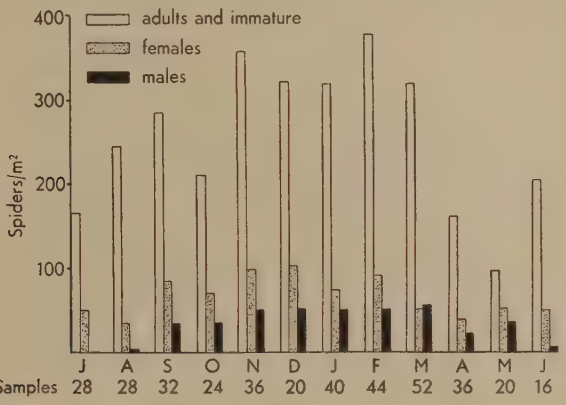

Fig. 5. The population density of *Hahnia nava* in quadrat samples from habitats A, B and C.

Pachygnatha degeeri (a common aeronaut) and a probable immature specimen of *Enoploglatha thoracica*. The remaining thirteen included the following species which were trapped or taken in the quadrats in large numbers: *Agroeca proxima*, *A. brunnea*, *Asagena phalerata*, *Cicurina cicur* and *Hahnia nava*. The most remarkable of these is *Hahnia nava* (Agelenidae) which in numerical abundance was second only to *Tapinocyba praecox* of all the species recorded in the study area. This species has a very distinctive shape and because no other *Hahnia* sp. was recorded during the period of study, it was possible to identify all immature and juvenile specimens. The population density over a two-month period is shown in Fig. 5 and in common with many other 'litter' species the highest values were recorded in the winter months. *Tapinocyba praecox* has a well-marked annual cycle, with the sudden appearance of large numbers of adults in September and October, followed by a gradual fall-off. *Hahnia nava*, on the other hand, has a more extended breeding season and the population changes are slower; thus from November to March, there is scarcely any fluctuation in the number of males, and apart from October, the monthly population density of immature spiders was always higher than that of the adults (Table 7). Although an occasional *Hahnia*

nava was taken in the pitfall traps, not a single specimen was caught on the canes, or seen anywhere but in its characteristic vegetation stratum. If population density is an important factor in inducing aeronautic behaviour, it clearly does not operate on *Hahnia nava*. Both these species and *Tapinocyba praecox* were abundant in the *Festuca* turf. Both were seldom taken in the pitfall traps so ground activity is slight. One readily disperses by aerial means, while *Hahnia nava* never appears to leave its chosen habitat.

Table 7. *Monthly population densities (spiders/m²) of adults and young of* Hahnia nava

	J	F	M	A	M	J	J	A	S	O	N	D
Adults	121	140	102	57	86	52	48	37	116	101	146	153
Young	197	238	205	104	109	152	117	206	170	98	212	168

(*e*) *The aeronautic catch in woodland*

Five greased canes were placed a few yards within the mixed deciduous woodland, which lies to the northern boundary of the study area (Fig. 1). These canes were 4 to 5 yd from the edge of the wood and a further 4 yd from the nearest cane in area C. Regular catches were taken from 14 December 1951 to 14 May 1952. Table 8, which illustrates the total catch for each month from December to May, shows a steady increase in numbers in the spring and early summer, and as with the main aeronautic catch this is partly a response to rising temperatures,

Table 8. *Catch per month of all spiders on five woodland canes*

January	February	March	April	May	December
3	11	31	41	46*	10

* First two weeks of May only.

which makes greater activity possible, but partly due to the appearance of new spiders in the catch. The two most numerous species were *Savignia frontata* and *Theridion pallens*. None of the former was taken after 16 April and none of the latter before this date. In the latter half of April and the first half of May *T. pallens* was very numerous and during this period with the coming of warm weather, the total catch number in this habitat was increased by non-aeronautic woodland species, e.g. adult males of *Linyphia peltata* which were actively searching for mates, by immature lycosids, and males of *Meta segmentata*.

The following seven aeronautic species were taken on the grassland canes but not on those in the wood: *Araeoncus humilis*, *Cnephalocotes obscurus*, *Wideria antica*, *Oedothorax apicatus*, *Micrargus herbigradus*, *Tiso vagans*, and *Dismodicus bifrons*. The most numerous of these was *Cnephalocotes obscurus*, of which twenty-four specimens were taken in the cane catch. Several other species which were recorded in both habitats were much less common in the woodland catch, even when the numbers were multiplied by a factor to give an estimate of the expected total if there had been twenty-four canes in the wood as there were in the grass.

Six such species are recorded in Table 9. *Theridion pallens* was very much more numerous in the woodland as has already been stated, while the comparative numbers of the remaining four species do not show much difference.

Table 9. *Catches of common aeronauts from woodland calculated for twenty-four canes for comparison with those from grassland*

The numbers taken on five canes in the wood are shown in parentheses.

	Woodland	Grassland
Meioneta rurestris	9·6 (2)	19
M. mollis	24·0 (5)	26
Savignia frontata	81·6 (17)	107
Cnephalocotes obscurus.	0	24
Erigone dentipalpis	19·2 (4)	16
E. atra	19·2 (4)	41
Tapinocyba praecox	9·6 (2)	75
Bathyphantes gracilis	14·4 (3)	42
Pachygnatha degeeri	9·6 (2)	12
Theridion pallens	211·0 (44)	30
Lepthyphantes tenuis	9·6 (2)	10

(*f*) *A comparison of the catches from the three grassland habitats*

During the period when aeronautic spiders were trapped on the greased canes it was realized that they could be caught in two ways, either while floating through the air on a strand of silk or when climbing up the canes before becoming airborne. There is little doubt that both of these methods contributed to the catches though the importance of each varied according to species. Table 10 lists the identified aeronauts from the canes in each of the three grassland habitats and it is clear that certain species predominated in each. *Tapinocyba praecox* is a species which can be recognized in the field and it was noticed on several occasions that numbers of trapped specimens were grouped round the base of the grease band, suggesting that they had climbed up the cane rather than been carried there by aerial drift. The population density of this species in the turf habitat was very much greater than in either of the other two habitats and the figures in Table 10 show that the aeronautic catch was also much higher. The catches of several other species can be explained in this way: *Cnephalocotes obscurus* was much more numerous in the *Brachypodium* and *Festuca* turf and was taken only on the canes in these areas; *Erigone atra*, *E. dentipalpis* and *Araeoncus humilis* were caught more frequently on the canes in habitat C where they were also more numerous on the ground. The cane catch of *Erigone atra* suggests that it has a wider distribution in habitats A and B than has *E. dentipalpis* and the results from the turf samples bear this out.

Conversely *Theridion pallens* was only twice taken in the quadrat samples (summer) but many reached the canes by aerial drift from the nearby wood. This would explain why the canes in habitat C, which were nearest to the trees, caught a considerably larger number of this spider than those which were situated further away. It is likely that *Theridion pallens* was able to float greater distances because it became airborne from tree foliage, whereas the linyphiids had to climb up from the ground. Although the study area is situated on a slope facing south-

west, it is completely surrounded by trees or bushes which must give it a good deal of shelter.

A considerable amount of drift is shown in several other species, although the aeronautic catches are in general agreement with their population densities in the three areas. *Bathyphantes gracilis* is much more common where there is a thick plant cover on the ground, and only one specimen was taken in the quadrat samples from area C. Nevertheless, the canes in this habitat caught fourteen specimens from December to May. Similarly *Savignia frontata* was considerably more numerous in the *Brachypodium* and *Festuca* but was still caught in numbers on the canes in area C.

Table 10. *Catches of aeronautic spiders from each habitat in the grassland area*

A, pure *Brachypodium pinnatum*;
B, a thick turf, mainly *Festuca rubra*;
C, thin vegetation over coral rag limestone, mainly *Camptothecium lutescens* but many herbs and grasses.
The totals for A and C (six canes each) have been doubled for comparison with B which had twelve canes.

	Habitats		
	A	B	C
Bathyphantes gracilis	28	17	14
Lepthyphantes tenuis	6	4	4
Pachygnatha degeeri	8	6	4
Tapinocyba praecox	18	65	2
Savignia frontata	70	63	50
Cnephalocotes obscurus	14	17	0
Meioneta mollis	6	15	16
M. rurestris	10	6	16
Erigone atra	6	21	34
E. dentipalpis	6	3	20
Araeoncus humilis	4	9	20
Theridion pallens	12	11	26
Oedothorax apicatus	0	0	2
O. fuscus	0	1	0
Wideria antica	4	1	0
Micrargus herbigradus	0	1	0
Tiso vagans	0	1	0
Dismodicus bifrons	2	0	0

The influence of the prevailing south-west wind may be responsible for the distribution of the aeronautic catch of *Meioneta mollis*, which was much more frequent in the *Festuca* turf than anywhere else, but was caught in nearly equal numbers on the canes in areas B and C (Fig. 1). The population densities and habitat preferences of grassland linyphiids will be discussed in another paper.

AERIAL DISPERSAL IN RELATION TO THE WEATHER

(*a*) *Introduction*

Throughout the numerous references in the literature to mass aerial dispersal by spiders, the weather conditions described nearly always follow the same pattern. Braendegaard (1937) made observations in mid-July on a day which he says 'was

the first real summer's day with bright sunshine'. Nielsen (1932) makes particular reference to calm sunny days in October; Bristowe (1929, 1939), Braendegaard and others fully appreciated the significance of such weather, and explained that under these conditions the ground temperature rises rapidly causing ascending currents of air on which the spiders float away. Bristowe (1939) discusses this behaviour in some detail and arrives at a physiological explanation. He suggests that during the cold nights of late autumn and early winter the aeronautic Linyphiidae, which live in the ground vegetation, become conditioned to low temperatures, so that the rise in temperature on a calm sunny morning proves uncomfortable if not intolerable, and they are prompted to seek cooler situations at the tops of vegetation. This discomfort, he says, may perhaps be enhanced by the prevailing high humidity in conjunction with the rise in temperature. Nielsen (1932) and Braendegaard (1937) also make the latter suggestion.

More recent studies suggest that some modification of these views may be necessary. It is known that the adults of common aeronautic linyphiids disperse by aerial means during the summer when the conditioning mechanism described above does not take place; Braendegaard (1937) himself described dispersal in mid-July, while Owen & Le Gros (1954) show that during the same month in 1944 and 1952 swifts caught large numbers of common aeronauts, including 443 *Erigone atra*, 227 *Lepthyphantes tenuis* and 158 *Erigone dentipalpis*. Active dispersal has been observed in the study area at Wytham on a mild day in January 1952 when the sky was overcast. It also appears likely that high humidities with or without high temperatures are normal in the 'litter' stratum of thick ground vegetation, where the wet, dead plant material is largely protected from evaporation and maintains a near-saturated atmosphere for much of the year.

Although some linyphiid aeronauts live in places where the ground vegetation is very thin, and may be immediately affected by the rising surface temperatures on a sunny morning after a cold night, this is by no means the case for many others. If a spider lives deep inside a thick *Festuca* turf or in the litter of a tall growth of *Brachypodium pinnatum* very little solar radiation is able to penetrate, and the surface of the grass, not the ground, experiences a steep temperature rise. The warming of the deeper vegetation layers is very gradual and is also not uniformly distributed so that a spider experiencing discomfort from a rising temperature may find a cooler place a short horizontal distance away. In addition, if it climbed up the vegetation to emigrate by aerial means, it would have to pass through a zone of considerably higher temperatures before reaching a height at which it can float away. Again some aeronautic species, such as *Theridion pallens*, which is typically arboreal, are subject to a completely different set of climatic conditions.

(*b*) *Surface and vegetation temperatures in relation to aerial dispersal*

In the early months of 1952, from 7 January to 26 February three resistance thermometers (thermistors) were placed in the litter layer of the *Festuca* turf habitat and in habitat C (thin plant cover over limestone). One thermistor was

placed inside the moss layer, a second on the surface and the third 3 ft above to record the air temperature. In addition, during the spring and summer of 1952 a continuous temperature recorder (Kempson & Macfadyen 1954) was used to make hourly temperature records in several places simultaneously in and on the vegetation of habitats C and A. These continuous records did not cover the period when catches of aeronautic spiders were made apart from a few days in March 1952, but they clearly illustrate the temperature profile of the two different types of ground vegetation.

Fig. 6 illustrates the numbers of spiders taken on the various collecting dates from 4 December 1951, to 14 May 1952, and the temperature taken in the

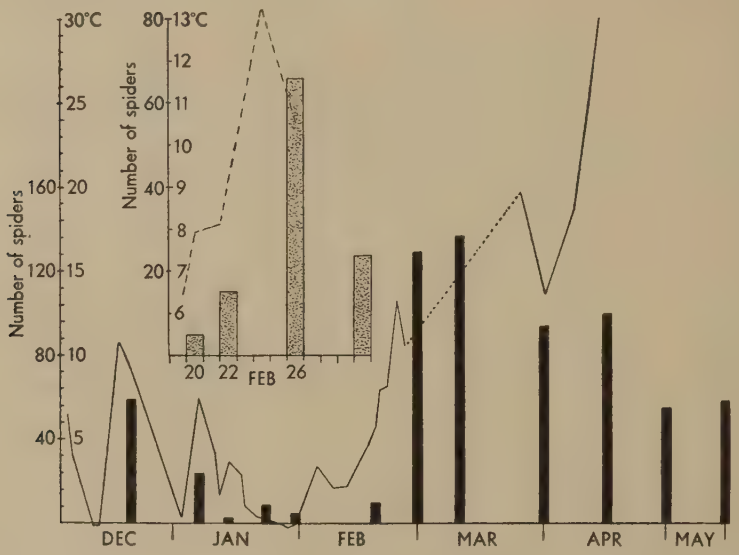

Fig. 6. Aeronautic catches in relation to 'litter' temperature in habitat C. Inset, detail of the catch made at the end of February. The curve shows the litter temperature at 1200 hours G.M.T.

litter of moss and other thin vegetation in habitat C. There is a clear coincidence between the increase in temperature and the increase in the number of spiders caught at this time of the year. Two comparatively warm periods in December and January result in higher catches than in the following period of 14 January to 19 February, when the litter temperature varied between 5·8° C and −0·3° C. However, even in the coldest period at the end of January with mid-day litter temperatures around 0° C, small catches were still made. After 19 February the weather became much milder and the mid-day litter temperature rose steadily until it reached 13·2° C on 24 February. The sudden increase in the number of aeronauts caught is shown on the inset histogram of Fig. 6. There was no catch on 19 February, 5 spiders on the 20th, 15 for the 21st and 22nd, and 66 for the four days 23rd to 26th. Although the weather continued mild the catch totals fell

off gradually. This particular example suggests that a sudden rise in temperature over a short period of a few days after a long spell of cold weather acts in some way as a releaser of aeronautic behaviour of more than normal intensity. It is as if the urge to migrate continues to develop even during the period of cold weather and that its cumulative effect is reflected in a particularly large dispersal with the commencement of a mild period.

Inspection of standard meteorological data for February and March provides some indication that favourable conditions for aerial dispersal existed during the period 21 to 26 February. On 20 February there were 5·7 hours of sunshine; on the 21st less than 2 hours; on the 22nd no sunshine was recorded and between 6·5 and 5·3 hours for the 23rd and 25th respectively; the 26th had 1 hour of

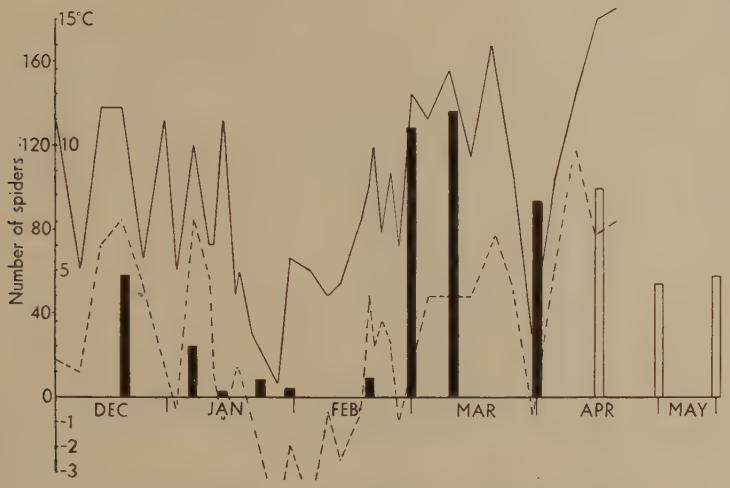

Fig. 7. Catches of aeronauts in relation to maximum and minimum screen temperatures at the Radcliffe Observatory, Oxford.

sunshine and this no doubt accounts for the fall in the litter temperature on that day. The wind speeds for this period averaged 4·8 m.p.h., so that the days were comparatively calm. The preceding four days, 16 to 19 February were cold and overcast (only 0·1 h of sunshine recorded) with an average wind speed of nearly 7 m.p.h. so that the period of aerial dispersal occurred during a spell of mild, comparatively sunny weather with a moderate breeze.

In Fig. 7 the maximum and minimum air temperatures from the Stephenson's screen at the Radcliffe Observatory, Oxford, are superimposed on the histogram of aeronautic catches. There is a general correspondence between small catches and low temperatures but the coincidence is not so clear as in Fig. 6. The litter temperatures fluctuated less than the corresponding air temperatures. Fig. 7 shows that as the days became warmer so did the nights, and that the diel temperature fluctuation during the warm period was no greater than that during the

Fig. 8. Temperatures in *Brachypodium pinnatum* in March and August: full line—in the litter close to the soil surface; pecked line—half way between the litter and the grass surface; dotted line—on the grass surface.

preceding cold period. It follows that the difference between the night and day temperatures cannot itself be responsible for activating aeronautic behaviour.

Fig. 8 shows extracts from the continuous temperature record for March and August respectively. In each case the hourly change of temperature in three different strata of a sward of *Brachypodium pinnatum* in area A is shown for 48 hours. These graphs clearly demonstrate the great fluctuation in temperature on the grass surface, while in the litter the temperature range is considerably less and the change is more gradual. The days illustrated (26 and 27 March), were both cool sunny days with 8 and $7\frac{1}{2}$ hours of sunshine respectively. During the night the *Brachypodium* litter was as much as 11° C warmer than the grass surface. The

early morning sunshine on the 27th began to warm the grass surface between 0700 and 0800 h while the air between the leaves and the litter also responded rapidly. The litter temperature increased slowly, but did not rise steeply until between 1100 and 1200 h. At any time between 0930 and 1630 h a spider climbing up the grass stems would have passed from a cooler to a warmer zone. Unfortunately there is no continuous temperature record for the period 19 to 26 February. In mid-August the litter layer may be the coolest zone night and day, as it was on the 15th-16th, but aeronautic behaviour may be marked in spite of the change in temperature profile.

Although high temperatures are probably the greatest single influence in stimulating aeronautic behaviour, the other weather conditions such as wind speeds are probably of considerable importance. Geiger (1950) discusses air movements and eddy diffusion close to the ground on calm sunny days. He says that if there was a laminar air flow over the surface of the ground, spores, seeds (and in this case, spiders) would not rise above their level of liberation. However, thermal stratification on a sunny day causes a constant movement upwards of warm parcels of air. The turbulence resulting is weak for about the first metre above the ground but then there is a great increase up to about 5 m. This may explain why emigrating spiders find it necessary to climb up the vegetation (and up the canes) before attempting to become airborne. There is obviously a limit to the weight of individual spiders which can be carried away by this type of eddy diffusion. Most of the small species emigrate as adults or when nearly adult, but the larger species must disperse as juveniles. A number of large and medium-sized spiders construct their egg cocoons in a higher vegetation stratum than where they normally live. *Agroeca proxima* and *A. brunnea* live close to the ground within the surface vegetation but their cocoons are found on tall grass stems or other plants projecting above the herb layer. *Xysticus ulmi* and *Marpissa pomatia* construct their cocoons on the flower heads of *Phragmites communis* while they live much lower down in the vegetation before they are mature. This behaviour is probably an adaptation to make dispersal by the young easier.

DISCUSSION

The most obvious point which emerges from the study of the nine aeronautic species discussed is the variety of activity patterns and the many different types of life-history. It clearly emphasizes how little is known about the biology of the smaller species of spider. In analysing the data presented for these nine species an initial separation can be made into those which show a peak in ground activity and those which do not, or in which such activity is very weak, as follows: *Tapinocyba praecox*, *Erigone atra*, *Savignia frontata* and *Meioneta mollis* show no or very little ground activity; *Erigone dentipalpis*, *Cnephalocotes obscurus*, *Meioneta rurestris*, and *Bathyphantes gracilis* show marked peaks in ground activity. Those species for which no ground activity has been recorded appeared to have a dispersal period during the time of highest population density or soon after. Species

with a ground activity peak and their period of maturity confined mainly to the winter may disperse either in spring, if the ground activity is in the autumn or early winter, or at the same time if both are in the spring. *Erigone dentipalpis*, which does not fit either of these categories, has an extended period of maturity covering most of the year, but there is a marked spring ground activity peak and though aerial dispersal takes place in nearly every month of the year, the largest numbers of aeronauts appear in late summer, autumn and early winter. None of those species having a ground activity peak in the autumn has an aerial dispersal period at the same time. The latter activity is delayed until the late winter or spring.

In cases where there is no clear population density peak and there is an extended period of maturity (*Lepthyphantes tenuis*), the dispersal period is also prolonged, though it may be most intense at a particular season. *Bathyphantes gracilis* also falls into this category, adults being commonly taken in every month of the year, but the ground activity peak in late summer and the spring dispersal are more marked than in the equally common *Lepthyphantes tenuis*. At the other end of the scale is *Cnephalocotes obscurus*, which shows sharper defined dispersal periods and population peaks, though at least some adult specimens may be taken in nearly every month of the year. The activity peaks occur at a time when the population density of adults is falling rapidly and the same is true for *Savignia frontata* with respect to aerial dispersal. The life-history of these two species appears to follow a well-marked annual cycle, though any reconstruction must be to a large extent hypothetical.

Taking *Cnephalocotes obscurus* as an example and referring to Fig. 3, it is clear that the main hatching months are June, July and August, when juvenile or very young spiders make up the largest proportion of immature specimens. In June *Cnephalocotes obscurus* is not represented in the grass samples by adult spiders. Thereafter mature specimens increase in number until a peak is reached in October, two months after the juvenile peak. The secondary peak in population density in March can only be explained by the retarded hatching of a proportion of the eggs, which overwinter, or by the development of some of the young ceasing in early winter before the last moult, and then most of these spiders becoming mature by shedding the last skin in early spring. It is known that several lycosid species overwinter mainly in the subadult stage, so that with the coming of warmer weather, the last moult takes place and the bulk of the population becomes mature in a relatively short time. Fig. 3 presents some evidence of a small February peak of juveniles and this may be the late-winter hatching. *Cnephalocotes obscurus* can therefore be described as having an extended winter maturity period. There was little or no ground movement during the winter of 1951-52, but in April the pitfall catch suggests sudden intense burst of mating activity which is maintained at a considerably lower level throughout the summer. In the same month and in March there was an active dispersal by air, which was not recorded at any other time. In this case, the mating and dispersal periods seem to be closely related and although the male was by far the most active of the sexes on the ground, slightly

more females were caught on the canes. After mating has taken place, one can understand that it would be a greater advantage to the species if more females than males dispersed, so that the young are reared in new localities.

Summarizing, the life-cycle of *C. obscurus* can be described as a summer egg-laying and hatching period, an autumn growth period, extending possibly to early

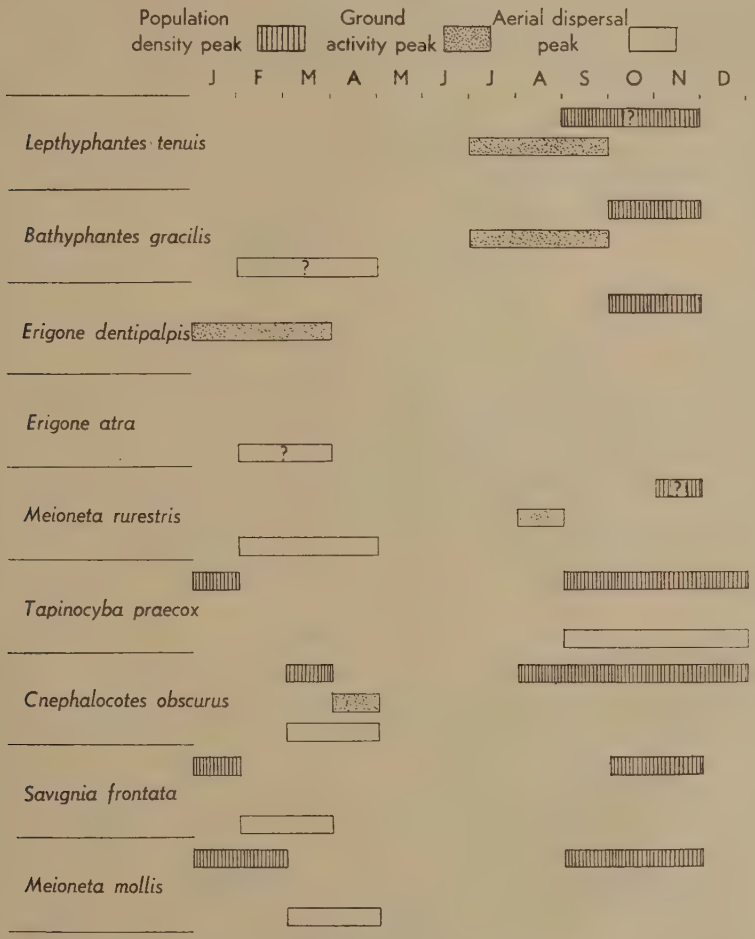

Fig. 9. A summary of the population density, ground activity and aerial dispersal peaks.

spring, a largely adult winter population and finally an active period of mating and dispersal in the spring before egg-laying. It is suggested that the basic life-history plan of the other eight species is similar in that individuals do not live for much longer than a year, but there is little similarity in the time of occurrence of activity periods, peaks in population density and their duration. It is also clear that aerial dispersal is an established part of the breeding-cycle, taking place at

different periods according to the species concerned, and related in some way to breeding activity and in some cases to population density. In Fig. 9 a brief summary is presented of the data for aerial dispersal, ground activity and population density. In each case only the peak months are illustrated and not the duration of each activity or of the period of sexual maturity.

It seems likely that temperature is the initial stimulus and most important factor prompting aeronautic behaviour during the colder months of the year, providing the species concerned is biologically ready to disperse. It is shown that the habitat of species living within the herb layer is warmed only slowly by the sun's rays but that once the spiders begin to climb upwards higher temperatures are met with as they reach the surface of the vegetation. This temperature gradient may be of importance in stimulating this behaviour as well as the initial rise in temperature in the 'litter'.

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SUMMARY

1. A distinction is made in the literature between the dispersal, mainly in the summer, of immature spiders from many different families, and the aeronautic behaviour of the Linyphiidae which takes place chiefly during the colder months and in which adults predominate.

2. The dispersal behaviour of the spider population of a small area of limestone grassland (three types) near Oxford was studied in relation to ground activity and population density during a twelve-month period.

3. The dominant species in the aeronautic catch vary according to the season. The dispersal activity of nine common aeronauts living in the herb layer is described in relation to ground activity and population density.

4. Although dispersal of linyphiids in the winter months is mainly by adult spiders, a proportion of immature spiders was recorded in each month from December to May, except January, when the catch was very small. Females predominate in the aeronautic catch.

5. The spider population of the study area included many species living in the herb layer, which did not disperse by air, although several were numerically abundant.

6. The aeronaut catch in adjacent woodland differs in species composition and numbers from that in the grassland; those in the three types of grassland also differ.

7. During the colder months temperature has a more important influence on aerial dispersal than have other microclimatic-factors. Aeronautic activity is inhibited during unfavourable weather.

8. The nine aeronautic linyphiids all show indications of an annual life-cycle, in which aerial dispersal is a normal event at a definite phase of the breeding-cycle. The twelve aeronautic linyphiid species most numerous in the herb layer reach a population density peak of adults in October.

9. Species having a peak period of activity on the ground in autumn, early winter or spring all disperse in spring. Species having no such period disperse during or soon after the peak of population density. Some species have an extended period of maturity and no marked peak of population density; these disperse and are active on the ground at all times.

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THE ANIMAL COMMUNITIES OF THREE AREAS OF PIONEER HEATH IN SOUTH-WEST ENGLAND

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The animal ecology of heathlands, although a large proportion of the British Isles is of this type vegetation, has failed to receive the recognition that botanists have given the floral component of this association. In 1926 Richards in his study of the animal communities of a sequence of plant successions at Oxshott Heath, Surrey, drew attention to the dearth of systematic studies into the structure and turnover of heathland communities. Unfortunately the papers subsequently appearing were both sporadic and more limited in scope. Diver & Good (1934) briefly described the survey work proposed and in progress at Studland Heath, Dorset, whilst Diver & Diver (1933) and Lack & Venables (1937) discussed the ecological relationships of the Orthoptera and birds respectively of this region. Cheetham (1942, 1943) considered the population changes experienced in a quadrat 20 m square of *Calluna* on Smearsett Copys, Yorkshire, from April 1942 to March 1943. None of these later authors made a concerted attack on determining, qualitatively or quantitatively, the composition of this habitat as a whole as was done by Richards (1926). More recently Pearsall (1950) has aimed at bringing into perspective the roles of animals and plants of the heathland community.

This survey arose as an aspect of the author's work into the bionomics of *Dilta littoralis* (Wom.) (Insecta, Thysanura), a common inhabitant of certain heaths in Devon and Hampshire. Other phases, including accounts of the microclimate of *Calluna* and the autecology of this insect, have been published elsewhere (Delany 1953, 1954). The following lists represent collections made over the period November 1950 to September 1951 in three localities in south-western England, each having *Calluna* as one of the major members of its community. The project attempted to obtain as complete a picture as possible of the animals accompanying pioneer heath and did not limit itself to individuals of any particular group, size or species. It was incidental, or possibly the result of the techniques adopted, that the organisms obtained were all arthropods. Only pioneer heath was selected as the low stature of the included plants rendered them more readily workable than the taller, thicker vegetation.

The wide size-range of the animals collected necessitated the application of two sampling methods. The larger individuals whose overall body length exceeded approximately 5 mm were collected by hand, and the smaller forms extracted

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from their accompanying litter through a Tullgren funnel. For convenience these two faunistic elements have subsequently been referred to as mesofauna and microfauna (*sensu* Fenton 1947) respectively. A metal quadrat was used throughout in determining the size of the area sampled. For the mesofauna a quadrat 0·5 m square was thrown at random usually fifty times in the course of a single day's sampling, and by careful hand collecting the fauna was removed from the enclosed areas. It was found adequate in the case of the microfauna to remove the litter beneath a clump of vegetation from an area only 10 cm square. This litter composed for the most part of fallen *Calluna* leaves formed a narrow stratum rarely exceeding 1 cm in depth. Within a few hours of removal the material was placed in the extracting funnel where it was exposed for twenty-four hours to the light of a 40 W bulb 15 cm away.

THE AREAS SURVEYED

The areas surveyed were located in south-east Devonshire, south Hampshire and the northern section of the island of Lundy in the Bristol Channel. All three were in lowlands, the maximum height above sea-level being attained in Devonshire where the Commons reached an elevation of a little under 600 ft. The vegetation in each appeared of homogeneous pattern with no extensive localizations of any of the more important plant genera.

(*a*) *Devonshire*

Surveys were undertaken in various communities of the heathland successions of a strip of common land lying 10-12 miles south-east of Exeter (Grid. ref. 30/08, 30/09). These habitats overlaid the rounded quartzite pebbles characteristic of the triassic Budleigh Salterton Pebble Beds. The plant ecology of the Commons has already been described in some detail (Delany 1954) but a few remarks pertaining to the vegetation of the regions under consideration would help elucidate their bio-physical structure.

Bicton Common I (Grid. ref. 30/034855). Here, the grass *Agrostis setacea* Curt. was in process of displacement by *Calluna vulgaris* Salisb. A large proportion of the ground had no plant cover, this resulting in the exposure of the underlying pebble beds. The grass *Molinia caerulea* Moench. was present in limited quantity.

Bicton Common II (Grid. ref. 30/034855). This vegetation represented a wetter and slightly more mature stage of the preceding association. It was of greater stature and the decline in the quantity of uncovered ground corresponded with an increase in the amount of *Ulex gallii* Planch. and *Molinia caerulea*.

Bicton Common IV (Grid. ref. 30/034859). This sector was composed essentially of pioneer *Calluna* with *Ulex*, *Erica*, *Molinia* and *Cladonia* as equal sub-dominants.

Colaton Raleigh Common (Grid. ref. 30/049888). Dominated by *Ulex* this area contained rather denser vegetation than any other considered. *Calluna* and

Erica were present in appreciable quantity but the grasses *Molinia* and *Agrostis* were almost completely lacking.

Large sections of the Commons were used during the war by the military and since then have suffered the rigours of periodic burning. As a result mature Callunetum has hardly had enough time to establish itself on a large scale. Rabbits restricted the growth of herbage through widespread grazing and apart from a few horses were the only larger herbivorous vertebrates inhabiting the Commons.

(*b*) *Hampshire*

The selected heathland was located on White Moor (Grid. ref. 41/31) one mile east of Lyndhurst where it rested upon the sandy, oligocene Middle Headon Beds. An area was arbitrarily subdivided into four sections each supporting a distinctive vegetation pattern. Their differences were those experienced in the course of a 25 ft drop from the uppermost level (A) to the lowermost (D). As in Devon these heaths were used extensively during the war by the military. Their tracked vehicles did considerable damage to the vegetation, from which it was only just beginning to recover at the time of the survey. In these parts of the New Forest the land was fairly heavily grazed by cattle, ponies and rabbits.

By assessing the percentage cover furnished by each of the constituent plant genera it was possible to express quantitatively, the floral composition of the above areas. To obtain these figures a quadrat 0·5 m square divided by string into twenty-five equal squares, was thrown fifty times in each locality. By looking directly over the centre of the squares the proportional coverage of the included plants could be determined fairly accurately. Table 1 shows the means of fifty such readings for each of the habitats studied.

(*c*) *Lundy*

Lundy can be described as a long, slender piece of granite emerging almost vertically up to 400 ft above the Bristol Channel and having an outcrop of slate appended to its south-east tip. The island extends roughly 3 miles from north to south and between $\frac{1}{4}$ and $\frac{3}{4}$ mile from east to west. Exposed to the full force of the prevailing south-westerly winds the comparatively level upper surface affords no shelter for the growth of trees and shrubs, and in consequence most of this portion of Lundy is covered only by grassland and heath. Estimates of the animal populations were made in an area of low, dense *Calluna* between 7 and 10 cm high immediately north of Threequarter Wall. A subjective estimate of the plant canopy suggested a coverage of 80-90% *Calluna* unaccompanied by other plants; the remainder of the ground was not covered by vegetation. In the early 1930s the northern half of the island suffered from a serious and prolonged fire which is reputed to have burned over a period of months and resulted in the complete destruction of the thin carpet of vegetation. The severity of this fire considerably hampered the re-establishment of the vegetation and even at the time of this survey large tracts of ground were devoid of plants and nowhere could they be

Table 1. *The percentage cover provided by the principal plant genera of the Devonshire Commons and Hampshire Heaths*

	Calluna	*Ulex*	*Erica*	*Molinia*	*Agrostis*	*Pinus*	*Cladonia*	Open	Water	Mean height of vegetation (cm)
Bicton Common I (Devon)	32·3	4·0	6·4	19·1	4·9	0·1	—	32·1	—	4
Bicton Common II (,,)	35.1	14·1	11·1	25·0	4·7	0·1	2·3	7·5	—	10
Bicton Common IV (,,)	58·2	9·1	9·1	8·9	0·2	—	11·0	3·6	—	6
Colaton Raleigh Common (Devon)	26·2	39·2	31·7	1·5	1·1	—	—	—	—	32
White Moor A (Hants)	45·2	0·2	9·9	3·4	—	—	—	41·3	—	7
White Moor C (,,)	42·0	0·1	5·0	4·6	—	—	0·1	48·2	—	8
White Moor D* (,,)	9·7	0·2	21·0	—	—	—	0·1	35·6	0.9	7

* This includes 16.6% of a mat of vegetation composed of two species of *Carex* and a grass.

regarded as beyond the pioneer stage. The area was grazed mainly by deer and ponies.

RESULTS

Lists appear in Tables 2 and 3 where the genera of each group have been placed in alphabetical order. Although the three areas investigated were in the same geographical region and of similar floral composition, slight differences nevertheless existed between them. Some, such as the variations in soil type were more readily observed. A light sandy soil occurred in Hampshire, a fairly heavy loam intermixed with the pebble beds in Devonshire and on Lundy a shallow, gritty soil overlay the granitic bed-rock. No determination of the drainage patterns or the water retentive powers of these soils was made. It appears probable that these factors would not all be identical and in consequence would separately influence the structure of the animal communities they supported. Such deviations could be expected within certain limits and allowances have to be made for them pending a very much more extensive survey.

The data lend themselves to critical examination from three main aspects. The faunal lists can help determine whether the animals inhabiting pioneer *Calluna* are to be found in a variety of habitats or are peculiar to this association. Comparison can also be made with heathland faunas in other localities and lastly, utilizing the population counts, a rough estimate of the relative importance of different species within the species network can be obtained. The soil-dwelling fauna has not been investigated and the microfaunal species can only be looked upon as the inhabitants of the upper surface.

(*a*) *The mesofauna*

Most of the species met with are of fairly general occurrence, only a few being restricted to heathland. Of the beetles, *Strophosomus sus* is a typical heathland species and *Cylindronotus laevioctostriatus* is generally associated with pine trees. It appears a little unusual that this latter species should exist in relatively large numbers on the Devonshire heaths. The remaining species of beetles are ubiquitous and not limited to any particular habitats. Similarly, most of the spiders can be found in a variety of habitats outside heaths. Exceptions include *Xysticus audax*, a species of furze bushes, and *Clubiona diversa* and *C. trivialis*, both typical of heaths. As a group the Hemiptera appear to contain the highest proportion of heath species; *Ischnocoris angustulus*, *Macrodema micropterum*, *Nabis ericetorum*, *Rhyparochromus pini*, *Scolopostethus decoratus* and *Ulopa reticulata* all fall within this category.

Richards (1926) separated his Callunetum species into two main groups, those found only in older, longer established *Calluna* and those in the less mature more typical Callunetum. As might be expected, the foregoing lists resemble the latter more closely than the former. Twenty of the species found in south-west England also occurred in the less mature *Calluna* whereas only five were shared with the older vegetation. The mesofauna of pioneer heath apparently consists largely of

Table 2. *Total numbers of heathland mesofauna*

	White Moor C	Colaton Raleigh Common	Bicton Common I	Bicton Common II	Bicton Common IV	White Moor A	White Moor D	Lundy
Date sampled (1951)	21 Jan.	26 Feb.	28 Feb.	3 Mar.	23 Apr.	20 Aug.	23 Aug.	3 Sept.
Area sampled (sq. m)	2·5	12·5	12·5	12·5	12·5	12·5	12·5	10
CRUSTACEA								
Philoscia muscorum Scop.	—	1	—	1	9	—	—	4
Porcellio scaber Latr.	1	—	1	1	—	1	2	—
COLLEMBOLA								
Entomobrya nivalis f. *multifasciata* (Tulb.)	—	—	—	—	—	—	1	—
Orchesella quinquefasciata (Bourl.)	1	—	—	—	1	—	—	—
Tomocerus longicornis (Müll.)	2	1	1	1	—	—	1	7
THYSANURA								
Dilta littoralis (Wom.)	8	—	16	6	15	35	43	—
ORTHOPTERA								
Chorthippus parallelus (Zett.)	—	—	—	—	—	—	1	1
Ectobius panzeri Steph.	—	—	—	—	—	2	4	—
Myrmeleotettix maculatus (Thun.)	—	—	—	—	—	1	1	
HEMIPTERA								
Dichrooscytus rufipennis (Fall.)	—	—	—	—	—	8	2	3
Ischnocoris angustulus (Boh.)	—	1	—	—	—	—	—	—
Macrodema micropterum (Curt.)	—	—	—	—	—	2	—	—
Megalonotus dilatatus (Herr-Schaef.)	—	—	—	—	1	2	—	—
Nabis ericetorum Scholz.	1	—	—	—	—	11	18	1
Rhyparochromus pini (L.)	—	—	—	—	—	—	—	2
Scolopostethus decoratus (Hahn.)	—	—	—	—	—	4	—	8
Trapezonotus arenarius (L.)	—	—	—	—	—	—	—	1
Ulopa reticulata (Fabr.)	—	2	—	1	—	3	—	3
Zicrona caerulea (L.)	—	—	—	—	—	—	—	1
COLEOPTERA								
Amara famelica Zimm.	—	—	—	—	—	1	—	—
Bradycellus harpalinus (Serv.)	—	1	—	—	—	—	—	—
B. ruficollis (Steph.)	—	1	—	—	—	—	—	—
Calathus melanocephalus (L.)	—	—	—	—	—	1	—	1
Cylindronotus laevioctostriatus (Goez.)	—	—	2	2	10	—	—	1

Table 2. (*cont.*)

	White Moor C	Colaton Raleigh Common	Bicton Common I	Bicton Common II	Bicton Common IV	White Moor A	White Moor D	Lundy
Date Sampled (1951)	21 Jan.	26 Feb.	28 Feb.	3 Mar.	23 Apr.	20 Aug.	23 Aug.	3 Sept.
Area sampled (sq. m)	2·5	12·5	12·5	12·5	12·5	12·5	12·5	10
COLEOPTERA (*cont.*)								
Feronia cuprea (L.)	—	—	—	—	1	—	—	—
Nebria brevicollis (Fabr.)	—	—	—	—	—	1	—	—
Notiophilus aquaticus (L.)	—	—	3	—	—	—	—	—
N. palustris (Duft.)	—	—	—	—	—	1	—	—
Odontonyx rotundatus (Payk.)	—	—	—	—	2	5	7	11
Philonthus fuscipennis (Mam.)	—	—	—	—	3	—	—	—
Quedius boops (Grav.)	—	—	—	—	—	—	—	1
Rhagonycha fulva (Scop.)	—	—	—	—	—	1	3	1
Staphylinus aeneocephalus Dege.	2	1	—	—	—	1	—	1
S. olens Muel.	—	—	—	—		—	—	2
Strophosomus sus Steph.	1	—	—	—	—	1	—	—
Tachyporus hypnorum (Fabr.)	—	—	1	—	—	—	—	—
Xantholinus longiventris Heer		—		—	—	—	1	1
LEPIDOPTERA								
Amathes agathina (Dup.) larvae	2	2	1	3	—	3	—	—
Eupithecia goossensiata Mab. larvae	—	—	—	—	—	1	—	—
E. nanata (Hueb.) larvae	—	—	—	—	—	—	—	1
Lycophotia porphyrea (Schiff.) larvae	—	—	—	—	—	3	12	125
HYMENOPTERA								
Formica fusca L.	—	—	—	—	—	5	1	5
Myrmica ruginodis Nyl.	—	—	—	—	—	1	—	—
DIPTERA								
Simulium ornatum Meig.	—	—	1	—	—	—	—	—

MYRIAPODA								
Lamyctes fulvicornis Mein.	—	—	—	—	—	—	—	1
Lithobius calcaratus C. L. Koch	1	—	—	1	1	—	—	—
L. lapidicola Mein.	—	1	1	—	—	1	—	9
Lithobius sp.	—	—	—	—	1	—	—	—
Polydesmis angustus (Latz.)	—	1	—	—	—	—	—	—
Schendyla nemorensis C. L. Koch	2	—	1	—	—	—	—	—
ARANEIDA								
Arctosa perita (Latr.)	—	—	—	—	—	4	—	—
Clubiona diversa O.P.-Camb.	—	—	1	—	—	—	—	—
C. trivialis C. L. Koch	—	—	—	—	—	—	3	—
Clubiona sp. juveniles	—	—	—	—	3	10	—	—
Drassodes sp.	—	—	—	—	—	—	—	2
Erigone promiscua O.P.-Camb.	—	—	—	—	—	—	1	—
Erigone sp.	1	—	—	—	—	—	3	—
Lepthyphantes obscurus (Black.)	1	—	—	—	—	—	—	—
Lepthyphantes sp.	2	—	—	1	—	2	—	—
Lycosa amentata (Clerck)	—	—	2	—	—	—	—	17
Lycosa sp.	3	1	15	5	9	—	14	1
Oonops pulcher (Temp.)	—	—	—	—	—	—	—	1
Oxyptila trux (Black.)	—	—	—	—	—	—	—	1
Oxyptila sp.	—	—	—	—	—	—	1	1
Pachygnatha degeeri Sund.	—	—	—	—	—	—	—	5
Pisaura mirabilis (Clerck)	—	—	—	1	1	—	1	—
Stemonyphantes lineatus (L.)	4	—	—	—	—	6	15	—
Stemonyphantes sp.	—	—	—	—	—	2	—	—
Tegenaria sp.	1	—	—	—	—	—	—	—
Theridion bimaculatum (L.)	—	—	—	—	—	—	1	—
T. denticulatum (Walck.)	—	—	—	—	—	—	1	—
Tibellus oblongus (Walck.)	1	—	—	—	—	—	—	—
Xysticus cristatus (Clerck)	1	—	—	—	—	—	—	27
X. audax (Schrank)	—	—	—	—	—	2	—	—
X. ulmi (Hahn.)	—	—	—		—	—	1	—
Undetermined juveniles	—	—	—		—	8	6	9
OPILIONIDEA								
Oligolophus agrestis (Meade)	—	—	—	—	—	11	29	—
O. hanseni (Kraep.)	—	—	—	—	—	1	—	—
Opilio parietinus (Deg.)	—	—	—	—	—	—	—	2
Phalangium opilio L.	—	—	—	—	—	7	1	—

species adapted to a wide range of habitats together with a sprinkling of the more characteristic animals of this association. The introduction of further typical heath elements to the exclusion of the wider distributed species possibly occurs in later successional phases.

Brief mention has been made already of possible physiographic and biological differences between the habitats studied. This can be more fully appreciated, as far as the faunal component is concerned, when the data for Lundy and Hampshire are brought together to illustrate the relative numbers of the principal carnivorous and non-carnivorous species (Table 4). Both collections were made within fifteen days of one another in August and September 1951 at a time of year when mesofaunal populations could be expected to be high. On Lundy the variety of carnivorous species is not as great as in Hampshire. Even allowing for the smaller area sampled (10 sq. m as compared with 25 sq. m in Hampshire) the discrepancy still appears a little large to be accounted for solely on these grounds. Furthermore, the species best represented are not the same in the two localities; the most numerous predators on Lundy were *Xysticus* and *Lycosa* and in Hampshire *Nabis*, *Stemonyphantes* and the opilionids. The total of predators per square metre is much the same in both areas. By way of contrast, the number of individuals likely to fall prey to the carnivorous forms display considerable variation. The lepidopteran larvae on Lundy constituted the primary food source and covered the ground to the extent of 12·6 individuals/sq. m. The Hampshire habitats supported a much smaller gross population of herbivores and scavengers with the thysanuran *Dilta littoralis* the numerically predominant species. The reasons for these wide deviations in the numbers of non-carnivorous animals and the extent to which they are likely to fulfil the nutritional requirements of the rest of the fauna are not clearly understood. At the time of the survey meadow pipits (*Anthus pratensis*) were a common feature of the Lundy heath. Lack (1935) had previously reported them as being numerous on this section of the island and there can be little doubt that they would considerably decimate the caterpillar fauna. Skylarks (*Alauda arvensis*), also insect eaters, were claimed by Lack (1935) to be second in abundance, although at the time of the counts under discussion they were not very common. Birds were in general more common on Lundy than elsewhere.

For both sets of counts the ratio of non-predators to predators is surprisingly high and a balance is probably only ultimately attained through carnivore eating carnivore.

Little is known of the activity and behaviour of the animals observed. The majority, at the time of capture, were immobile and located at or near the base of the vegetation in well shaded situations. Caterpillars invariably inhabited the leafy twigs. Certain spiders, notably lycosids, were more active and the rapidity of their movement frequently made them difficult to capture. Unlike the rest of the mesofauna, they were prepared to traverse the open ground between clumps of heather when the effects of insolation were at a maximum. On warm days an appreciable temperature change takes place within a comparatively short horizontal distance. The measurement of microclimatic conditions on Devonshire

Table 3. *The total numbers of heathland microfauna*

Area sampled (sq. cm)	Bicton Common I 24 Nov. 1950 200	Colaton Raleigh Common 26 Feb. 1951 100	Bicton Common II 28 Feb. 1951 100	White Moor A 24 Jan. 1951 100	White Moor C 23 Jan. 1951 100
COLLEMBOLA					
Folsomia quadrioculata (Tullb.)	—	—	8	—	—
Friesia mirabilis (Tullb.)	—	—	1	—	—
Hypogastrura granulata Stach	—	—	1	—	—
Isotoma tigina (Nic.)	—	—	—	1	—
Isotoma sp.	2	—	—	2	—
Neanura muscorum (Temp.)	—	1	—	—	7
Onychiurus sp.	—	1	—	—	—
Pseudisotoma sensibilis Tullb.	—	1	2	1	1
THYSANOPTERA					
Taeniothrips (*Amblythrips*) *ericae* (Hall.)	13	4	1	3	1
DIPTERA					
Sciara sp.	—	—	—	—	1
Unidentified larvae	1	3	4	4	2
HEMIPTERA					
Psyllid nymphs	10	1	1	—	30
ACARI					
Oribatei					
Adoristes ovatus (Koch)	—	14	—	—	—
A. poppei (Oudms.)	2	—	—	—	—
Camisia segnis (Herm.)	—	25	—	1	—
C. spinifer (Koch)	—	—	3	4	—
Carabodes marginatus Mich.	—	—	8	12	—
C. minusculus Berl.	14	—	287	6	—
Ceratoppia bipilis (Herm.)	2	—	2	3	—
Chamobates sp.*	27	41	27	11	12
Hermaniella picea (Koch)	—	5	—	—	—
Humerobates rostrolamellatus Grandj.	1	—	—	1	—
Liacarus coracinus (Koch)	—	—	—	5	—
Nothrus silvestris Nic.	1	2	—	—	—
Oppia ornata (Oudms.)	9	12	4	7	8
O. nova (Oudms.)	—	—	2	1	—
O. insculptum (Paoli)	—	—	—	—	2
Oribatella calcarata (Koch)	1	3	—	—	—

* Dr. G. O. Evans informs me that this species cannot be identified with certainty with any of the known species of the genus and he is withholding further identification until a revision of the Oribatei, at present in progress elsewhere, is published.

	Bicton Common I	Colaton Raleigh Common	Bicton Common II	White Moor A	White Moor C
	24 Nov. 1950	26 Feb. 1951	28 Feb. 1951	24 Jan. 1951	23 Jan. 1951
Area sampled (sq. cm)	200	100	100	100	1000
ACARI (*cont.*)					
Oribella castanea (Herm.)	2	—	—	—	3
Odontocepheus elongatus (Mich.)	—	3	—	—	—
Parachipteria willmanni v.d. Hammen	—	—	4	—	
Pelops bilobus Sell.	—	—	—	1	2
Phthiracarus piger (Scop.)	—	—	—	3	
Scutovertex sculptus Mich.	—	—	—	1	
Suctobelba sarekensis Forss.	—	—	—	1	
Tectocepheus velatus (Mich.)	3	5	3	19	—
Tectoribates tecta (Mich.)	—	—	4	—	
Gamasides					
Amblyseius obtusus (Koch)	1	3	1	4	—
Cosmolaelaps claviger Berl.	—	—	—	1	—
Ologamasus calcarata (Koch)	—	3		—	—
Pergamasus crassipes longicornis Berl.	1	1	5	1	3
P. lapponicus Trädgh.		8	—	4	—
Rhodacarus roseus Oudms.	2	—	—	2	—
Zercon zelawaiensis Sell.	—	1	—	—	—
Z. arctuatus Trädgh.	—	1	—	—	—
Zercoseius spathuliger (Leon.)	—	—	—	2	—
Uropodina					
Olodiscus minima (Kram.)	—	—	—	2	—
Prostigmata					
Bryobia praetiosa (Koch) larvae	—	—	—	—	2
Cocceupodes clavifrons (R. Can.)	—	—	—	—	1
Cyta latirostris Herm.	—	—	—	1	—
Eupalopsellus ölandicus (Sell.)	2	—	—	—	—
Eupodes ?voxencollinus Sig. Thor.	—	—	—	1	—
Ledermulleria segnis (Koch)	1	1	—	—	—
Pygmephorus delanyi Evans	1	—	—	—	4
Stigmaeus callunae Evans	1	—	—	—	1
Acaridae					
Tyroglyphus farinae L.	—	—	1	—	—
Unidentified immature forms	110	127	128	110	71
MYRIAPODA					
Unidentified geophilids	—	—	—	—	2

heaths (Delany 1953) indicated a temperature difference of more than 10° C between the base of the *Calluna* and uncovered adjoining ground on certain summer days. The ground surface temperature beneath the *Calluna* was generally cooler and more even, during hours of daylight, than outside it. The relative humidity was almost invariably lower immediately above the surface of the open ground than in a corresponding position within the vegetation. Microclimatic measurements were made on White Moor (Delany, unpublished results) on 21 August 1951. As in Devonshire, a more even temperature was experienced as a result of the plant cover. The temperature profiles and fluctuations conformed to the same general pattern as those in Devonshire on 14 July 1951 (Delany 1953). The extent to which microclimate alone influences the distribution of an animal is difficult to assess. Higher susceptibility to bird predation and a greater chance of desiccation are possible reasons for an insect remaining in close association with vegetation during sunny spells.

Table 4. *Grouping of total numbers of commoner species of the mesofauna according to their feeding habits for Hampshire and Lundy in the late summer of 1951*

	Hampshire (Areas A and D combined)		Lundy	
	Total animals in 100 quadrats 0·5 m square	Population per sq. m	Total animals in 40 quadrats 0·5 m square	Population per sq. m
Predatory species				
Nabis ericetorum	29	1·16	1	0·1
Odontonyx rotundatus	12	0·48	11	1·1
Lithobius lapidicola	1	0·04	9	0·9
Clubiona spp.	13	0·52	—	—
Lycosa spp.	14	0·56	18	1·8
Stemonyphantes spp.	23	0·92	—	—
Xysticus spp.	3	0·12	27	2·7
Opilionids	49	1·96	2	0·2
Totals	144	5·76	68	6·8
Non-predatory species				
Dilta littoralis	78	3·12	—	—
Ectobius panzeri	6	0·24	—	—
Lepidoteran larvae	19	0·76	126	12·6
Totals	103	4·12	126	12·6

(*b*) *The microfauna*

The microfauna, composed for the most part of mites and Collembola, lives within the surface humus and deeper soil layers. Many of its members are concerned with the breakdown, directly or indirectly, of the plant fragments that steadily accumulate on the ground surface. Workers in the British Isles (Glasgow 1939, Ford 1937, 1938, Macfadyen 1952) have demonstrated the soil microarthropods to display population maxima somewhere between December and February and population minima during the summer months. On the basis of

these previous observations the six samples taken in Hampshire and Devonshire in the winter of 1950-51 are believed to be fully representative of the soil surface fauna.

The microarthropods in localities covering a wide range of plant associations have been compared with the present collections. The works referred to include those of Hammer (1944), Forsslund (1945), Weiss-Fogh (1948), Van der Drift (1950), Tarras-Wahlberg (1952-53), Macfadyen (1952, 1954) and Murphy (1953). A number of species, including *Carabodes marginatus*, *Ceratoppia bipilis*, *Oppia neerlandica*, *Tectocepheus velatus*, *Friesia mirabilis* and *Neanura muscorum*, are of widespread distribution irrespective of the soil type from which they have been taken. These species must be well adapted to a wide range of habitat conditions and Hammer (1944) has attributed the excellent integration of *Tectocepheus velatus* with its environments to its ability to vary its breeding-cycle in accordance with habitat variations. Of the Acari, the surface layers of Forsslund's (1945) *Vaccinium* shared ten species with the south-west England heaths, Weiss-Fogh's (1948) areas III, IV, H and *Calluna* (B) (i.e. those most closely resembling the south-west England vegetation) eleven, and Murphy's (1953) heaths of Allerston Forest, Yorkshire, seven. It appears anomalous that Forsslund making his collections in Swedish Lapland (and from a different type of vegetation) and Weiss-Fogh in Denmark should find closer agreement in the composition of their faunas with the present study than did Murphy whose work was undertaken in the British Isles and from similar plant litter. According to the literature reviewed several species are sporadic in their distribution; these include *Tomocerus longicornis*, *Adoristes poppei*, *Camisia spinifer*, *Hermaniella picea*, *Joelia cannexa*, *Oppia insculptum*, *Pelops bilobus* and *Scutovertex sculptus*. The non-oribatid mites have not been subjected to as many systematic investigations as the Oribatidae and Collembola and this lack of information renders impracticable thorough faunistic comparisons of this section of the fauna.

Carabodes minusculus was the most numerous microarthropod although in this case the figures are somewhat biased due to the presence of 287 individuals in a single sample; next in abundance came *Chamobates* sp., *Oppia ornata* and *Tectocepheus velatus*. The total number of Acari and Collembola collected in the microfaunal analyses have been classified according to feeding habits and summarized as populations per square centimetre: vegetarians and scavengers, 6·53; carnivores, 0·46; species of uncertain feeding habits, 0·09; juveniles of undetermined species, 5·46. The ratio of the number of known predators to the number of non-predators for this section of the microfauna is approximately 1 : 14·2. This is of a quite different magnitude to the mesofauna where the ratio is of the order of 1 : 1·2. Naturally, the populations of the meso- and microfaunas are closely interlinked and their separation is quite artificial. The discrepancy in their predator-prey balances could be adjusted by certain members of the mesofauna feeding disproportionately on the vegetarians of the microfauna. The importance of the more active organisms whose sizes range between 2 mm and 5 mm have possibly been misrepresented by the tabulated data. These organisms are too large to appear in

anything but very small numbers in the microfaunal samples and are sufficiently small and motile to evade capture at times of hand sampling. Within this category are many of the Hemiptera and particularly *Tomocerus longicornis* and *Orchesella quinquefasciata* among the Collembola.

The absolute populations of meso- and microfaunas cannot be compared without modification of one set of estimates as the microfaunal samples were taken exclusively from within the vegetation and the mesofaunal samples randomly from whole areas, quite considerable proportions of which were uncovered by plants.

DISCUSSION

Elton & Miller (1954) have summarized the theoretical and practical considerations involved in making an ecological survey of animal communities and propose a practical system for the classification of their habitats. Many of the suggested prerequisites for a comprehensive survey, such as the need for continuity of the project with a view to determining the dynamic processes within an animal community, are equally applicable here. Even from the small number of observations made in this study appreciable faunal differences can be detected between what at first glance may be taken for structurally similar habitats.

It seems quite possible that Elton & Miller's concept of centres of action is too simple and that even as rough and ready practical units, apparently similar centres of action may in fact conceal animal communities of very different structure. This survey supports the contention that it is inadequate to define the habitat of an animal community in terms of the vegetation type alone. Differences in topography, aspect and situation of the sampling areas, growth form of their constituent plants, soil structure, climate, the nature of the underlying rock, previous history of the habitats and their proximity to other vegetation types could each affect the structure of the animal community without necessarily producing any marked change in the plant carpet itself.

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SUMMARY

1. A survey of the animals inhabiting pioneer heath in Devonshire, Hampshire and on the island of Lundy were made between November 1950 and September 1951.

2. The larger organisms were collected by hand and the smaller ones extracted through a Tullgren funnel. In both cases the figures obtained were referable to a predetermined area of habitat. The species falling into these two groups (the mesofauna and microfauna respectively) have been listed separately.

3. The mesofauna was represented by a mixture of species, some characteristic of heaths and the remainder of ubiquitous habits. The numerically most abundant herbivores were not of the same species in Hampshire and on Lundy.

4. A relatively small number of species of the microarthropods are of widespread distribution.

5. Estimates of the total numbers of predators and non-predators have been compared for the two major faunistic components. The ratio is very much higher for the mesofauna than the microfauna.

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THE POPULATION DYNAMICS OF HOST SPECIFICITY IN *URCEOLARIA MITRA* (PERITRICHA) EPIZOIC ON FRESH-WATER TRICLADS

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(With 2 Figures in the Text)

INTRODUCTION

Urceolaria mitra (von Sieb) a peritrichous ciliate found on freshwater triclads has been recorded most commonly from *Polycelis tenuis* Ijima, *P. hepta* E.H- & Y. Melander (Hansen-Melander, Melander & Reynoldson 1954), *P. nigra* (Müll.) and *P. felina* (Dalyell). It has been found occasionally in small numbers on *Dugesia lugubris* (Schmidt), but has not been taken in this work from the other British freshwater triclads, viz. *Dendrocoelum lacteum* (Müll.), *Bdellocephala punctata* (Dallas), *Planaria torva* M. Schultze, *Phagocata vitta* (Dugès), *Crenobia alpina* (Dana) or *Dugesia tigrina* (Girard), a recently discovered American species, although only small numbers of some species, particularly *Planaria torva* have been examined. Earlier workers (see Keiser 1921 for references) have recorded it from *Dendrocoelum lacteum* and *Planaria torva* but it is evident that the epizoite thrives mainly on hosts of the genus *Polycelis*.

The biology and especially the population ecology of *Urceolaria mitra* have been described in some detail (Reynoldson 1950, 1951, 1955) and it is clear that the ciliate utilizes the host-produced water currents for feeding purposes and does no direct harm to the host. The life-cycle is straightforward, the epizoite remaining the greater part of its life on the host where it grows and multiplies. However, a small proportion of the population is continually leaving the host and these *Urceolaria* reattach after a few hours' free life, usually to another host. In this way *Urceolaria* infests the host's progeny. When *Polycelis tenuis* and *P. nigra* occur together in a pond the former always has a markedly higher population of *Urceolaria*. The explanation of this disparity in terms of population dynamics is the main problem tackled here. It can be said at the outset that careful examination of specific characters such as the number of denticles in the skeletal ring, number of striae per denticle, etc. (Fauré-Fremiet 1943) showed that there were no anatomical differences between the *Urceolaria* on the two hosts.

Three explanations with different biological emphases seem possible. First, the two epizoic populations may represent biological races and exhibit rigorous host specificity. Second, host specificity may not be absolute and some exchange may occur but nevertheless *Urceolaria* may be able to thrive better on one host

than on the other. Third, the presence of *Urceolaria* on *Polycelis nigra* may only represent an 'overflow' from *P. tenuis* and the epizoite may be unable to persist on *P. nigra* in the absence of the *P. tenuis* population. Each hypothesis is examined both by the analysis of field collections and by laboratory experiment.

While this work was in progress an additional species of *Polycelis*, *P. hepta*, has been described closely resembling *P. tenuis* and often occurring with it in ponds. The two species can only be distinguished by the examination of squash preparations of the reproductive organs or cytogenetically (Hansen-Melander, Melander & Reynoldson 1954). The ponds from which experimental animals were collected contained both species and their separation meant limiting experiments to adult animals and also allowing time for regeneration after examining squashes of the posterior region. However, the evidence showed that the urceolarian populations of both these flatworms were numerically and behaviouristically similar and need not be differentiated in their present context.

All field collections of *Polycelis tenuis* and *P. nigra* were kept in separate jars and examined for *Urceolaria* on the day of collection using the chromic acid technique (Reynoldson 1950). This technique was also used to provide flatworms free of epizoites for experiments. After treatment they were allowed a minimum recovery period of 24 h. Frequent checks were made on the efficiency of the method and in no instance has the treatment failed to remove all the *Urceolaria*. Large numbers of *Urceolaria* for experiments were obtained by brushing them from their hosts into a drop of water on a slide, using a camel-hair paint-brush. In comparative studies of the growth of *Urceolaria* and of host selection, flatworms of each species comparable in size and previous treatment were used. The separation of *Polycelis tenuis* and *P. hepta* was unnecessary for the solution of several of the problems examined here. Wherever this applies the term '*tenuis-hepta*' has been used to indicate the non-separation of these two species. Other special techniques are described in the appropriate section. Unless stated otherwise, all experimental material came from the local College or Vaynol ponds (Reynoldson 1955).

THE *URCEOLARIA* POPULATIONS OF *POLYCELIS TENUIS* AND *P. HEPTA*

The main morphological distinction of *Polycelis hepta* is the absence of adenodactyls. Fortunately records of the presence and absence of these have been maintained and it was possible to re-examine records of mature worms and to separate the two species. These provided data on the urceolarian populations of the two species which is summarized in Table 1. Although the data are based on small individual collections of worms (the problem had not emerged at the time) it is obvious that the urceolarian populations of each species are similar in the majority of localities; none of the pairs of averages differ significantly. Larger samples of the two species were taken on one day from College Pond, Memorial Science Buildings, Bangor, in February 1950. The average epizoic population on twenty-four *P. hepta* was 5·5, S.D. ±2·7; and on fifty-five *P. tenuis*, 5·7, S.D. ±3·3.

The difference between the means is not significant and it is concluded that epizoic populations of both species are similar in size.

Table 1. *The urceolarian populations of* Polycelis hepta *and* P. tenuis

Date of collection	Lake	Locality	Number examined		*Urceolaria* per worm	
			P. hepta	*P. tenuis*	*P. hepta*	*P. tenuis*
Feb. 1951	Coron	Anglesey	8	10	21·8	20·0
Aug. 1950	Bolam	Bolam, Northumberland	7	4	29·3	46·8
Aug. 1950	Sir Edward's	Capheaton, Northumberland	3	4	34·7	35·0
Aug. 1950	Harewood Hall	Harewood, Yorks.	4	5	63·3	69·8
April 1951	Coniston Cold Hall	Near Skipton	5	11	24·4	21·8
Aug. 1950	*Cleabarrow	Near Bowness	8	3	19·9	30·0
Aug. 1950	*Blelham Tarn		8	7	12·1	10·9
Aug. 1950	*Rather Heath	Near Kendal	8	3	21·4	30·0
Aug. 1950	High Wray Bay	Windermere	7	5	24·3	25·6
Aug. 1950	Boat House	Windermere	4	5	8·5	6·6
	Total		62	57		

* See Macan (1950), Fig. 1.

FIELD POPULATIONS OF *URCEOLARIA*

(*a*) *The relative density of* Urceolaria *on* Polycelis 'tenuis-hepta' *and* P. nigra

The most substantial data are derived from a study of population fluctuations in *Urceolaria* extending over a year in College Pond and over three months in Vaynol Park Pond, near Portdinorwic, Caernarvonshire (Reynoldson 1950, 1955). These have been supplemented by single counts or estimates from other localities (Table 2). There is also a large body of supporting qualitative data from different parts of the British Isles. While all the differences between the means of the *Urceolaria* populations of the two flatworm species in Table 2 are significant there is some variation in the ratio. The two results for College Pond also indicate that the ratio may vary considerably with time in the same habitat. This view is supported by the values of the ratio for individual weekly collections in Vaynol

Table 2. *The relative density of* Urceolaria *on* Polycelis nigra *and* P. 'tenuis-hepta' *in various habitats*

		Urceolaria per worm		Ratio	
		P. 'tenuis-hepta'	*P. nigra*	*P.t-h.* : *P.n.*	
1946-47	College Pond, Bangor	22·7	0·7	32·4 : 1	Data averaged over one year
May-Aug. 1948	Vaynol Pond, nr. Bangor	51·0	2·6	19·6 : 1	Data averaged three months
Oct. 1951	College Pond, Bangor	58·0	9·7	6·0 : 1	Special examination at urceolarian peak
Feb. 1951	Llyn Coron, Anglesey	21·8	3·5	6·3 : 1	Single collection
Apr. 1951	Tenley Lake, Coniston Cold, nr. Skipton	16·7	1·0	16·7 : 1	Single collection
June 1951	St. Germaines Loch, Glasgow	Abundant	Few	—	Single collection
July 1951	Loch Rusky, Perthshire	30-50	Few	—	Single collection

Park Pond (Table 10) which vary markedly from week to week. It is concluded that the denser populations of *Urceolaria* on '*tenuis-hepta*' compared with *nigra* are a constant feature of habitats containing both species.

(*b*) *Fluctuations of the* Urceolaria *populations*

These have been studied intensively for the *Polycelis 'tenuis-hepta'* population and it has been concluded that they are related particularly to rainfall and the resultant bacterial fluctuations (Reynoldson 1950, 1955). It is of interest to discover whether or not the fluctuations of the epizoic populations of both species are in step. The Vaynol Park data, extending over a twelve weeks' period when the *Urceolaria* population was fluctuating markedly, have been analysed. They suggest that the fluctuations of the two epizoic populations tended to be in step (Fig. 1) and the correlation coefficient measuring the agreement is significant

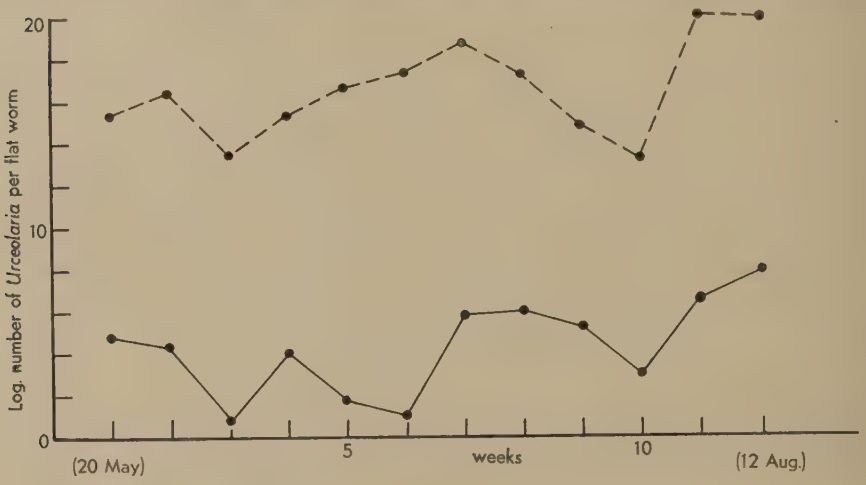

Fig. 1. The population trends of *Urceolaria* on *Polycelis 'tenuis-hepta'* (broken line) and on *P. nigra* (continuous line).

($r = 0{\cdot}706$, $0{\cdot}01 < P < 0{\cdot}02$). Although the period of observation is brief the results suggest that both populations are regulated by the same factors. However, this does not indicate which of the theories may be correct, since with each parallel changes could occur.

(*c*) Urceolaria *populations of isolated* Polycelis nigra *populations*

In many freshwater habitats the flatworm fauna consists of only *Polycelis nigra*. The epizoic fauna of such populations, particularly if there is good evidence for the long absence of *P. tenuis* and *P. hepta* is of interest in the present connection. The triclad fauna of Anglesey has been studied intensively and provides numerous examples of such host populations. Furthermore, the other two host species are rare on the island and have been recorded from only two lakes and one stream.

Data from sixteen ponds and lakes and eight streams carrying only *P. nigra* are available. The majority of these records are based on a single collection of about twenty flatworms but five of the lakes and several of the streams have been visited more frequently and at least sixty worms from each examined. In seven out of the sixteen still-water habitats and seven out of the eight streams *P. nigra* supported an *Urceolaria* population. The density of the epizoite was usually low (<10 per worm) but in some cases was comparable to those on *P. tenuis* and *P. hepta*. For example, in one stream *P. nigra* had an average population of 22 *Urceolaria* per worm while two of the lakes showed epizoic populations of 28 and 11. Evidently *P. nigra* is able to support *Urceolaria* in the absence of the other two host species. Thus the suggestion that the epizoic population of *P. nigra* is solely an overflow from *P. tenuis* or *P. hepta* seems unlikely. But the possibility remains that a specific *P. nigra* race may evolve in the long absence of *P. tenuis*. This has still to be explored.

The considerable number of negative records for *Urceolaria* from still-water habitats (nine out of sixteen) should be noted. Apart from data for Islay (Argyll) where *Urceolaria* was not recorded on any flatworm, negative records for *P. tenuis* and *P. hepta* are unusual. But how far this contrast is due to host or to more general conditions of the habitat cannot be determined at present.

SPECIFICITY OF THE *URCEOLARIA* POPULATIONS

The hypothesis that the epizoic populations of *Polycelis 'tenuis-hepta'* and *P. nigra* might be independent and the density difference due to factors inherent in each association was tested in an empirical but conclusive manner. The experiment was based on the fact that the epizoite disperses by becoming free-swimming at a relatively low incidence and reattaching to a host (Reynoldson 1951). Flatworms of both types cleaned of *Urceolaria* were exposed under equivalent conditions to reinfestation from an infested worm. Five cleaned specimens of *'tenuis-hepta'* and four of *nigra* comparable in size were kept in 200 ml of filtered pond water in Pyrex dishes 8·5 cm in diameter and 5 cm deep to which one infested *nigra* was added. The dishes were kept in the dark at 20° C and after seven days the urceolarian populations of the originally cleaned hosts were determined. The approximate number of *Urceolaria* on the infested worm was also noted at the beginning of the experiment and accurately at the end. The experiment was repeated ten times. A corresponding series was carried out with infested *'tenuis-hepta'* and to simplify statistical analysis five cleaned worms of each type were used. The experiment was repeated ten times. The results for each series are recorded in Table 3.

If host specificity is rigorous then in the series using infested *nigra*, only cleaned *nigra* should be reinfested, and similarly in those using infested *'tenuis-hepta'* only the latter. It is clear from the results that irrespective of origin the population of *Urceolaria* was always larger on *'tenuis-hepta'* and in this resembled field conditions. In each of the individual experiments a larger epizoic population was found on

Table 3. *The population of* Urceolaria *developing on cleaned* Polycelis nigra *and* P. 'tenuis-hepta' *from infested worms of both species as sources*

	Experiment number										Total
	1	2	3	4	5	6	7	8	9	10	
INFESTED *P. nigra* AS SOURCE											
Urceolaria on infested host:											
at the beginning	20	5	40	20	15	10	20	10	10	10	
at the end	64	15	64	46	5	4	12	0	2	26	
Urceolaria developing:											
on *P. nigra*	7	0	14	5	5	3	4	0	0	7	45
on *P. 'tenuis-hepta'*	63	57	62	82	16	44	48	20	14	15	421
Total	70	57	76	87	21	47	52	20	14	22	466
χ^2	33·60	45·49	20·89	52·89	*3·57	27·60	28·43	16·04	11·12	*1·46	
INFESTED *P. 'tenuis-hepta'* AS SOURCE											
Urceolaria on infested host:											
at the beginning	50	50	30	30	40	30	20	40	50	50	
at the end	225	250	120	185	166	105	43	170	210	270	
Urceolaria developing:											
on *P. nigra*	13	14	11	7	9	12	6	0	4	19	95
on *P. 'tenuis-hepta'*	59	136	61	13	57	178	16	103	71	131	825
Total	72	150	72	20	66	190	22	103	75	150	920
χ^2	29·40	99·22	34·72	*1·80	34·90	145·04	4·55	103·00	59·84	83·60	

* Not significant.

this host type and with three exceptions (* in Table 3) the χ^2 test showed that the difference between the two populations was markedly significant ($P<0{\cdot}01$ in most instances). It is concluded that the *Urceolaria* occurring on *nigra* and '*tenuis-hepta*' represent individuals of the same species with identical behaviour.

FACTORS RESPONSIBLE FOR THE CONTRASTED EPIZOIC POPULATIONS

As the basis for such analysis it has been considered that an urceolarian population becomes established in three steps, each of which may cause dissimilarity. Starting with free-swimming *Urceolaria*, the relative attractiveness of the two hosts was first measured by exposing simultaneously cleaned worms of each type to free *Urceolaria*. After the epizoite has attached there might be variation in its ability to remain on the host or, looked at in another way, in the dispersal rate. This formed the second problem which was examined by measuring the relative dispersal rates from the two hosts. Finally, it was also necessary to measure the population growth-rate of *Urceolaria* on each host. In this way it has been possible to decide empirically the contribution of each stage to the final epizoic populations of *Polycelis nigra* and *P.* '*tenuis-hepta*' when the hosts co-exist.

(*a*) *Attachment*

The initial technique used to determine the relative attractiveness of *Polycelis nigra* and *P.* '*tenuis-hepta*' was more elaborate than necessary and has been simplified since, but the results are none the less trustworthy. Pyrex dishes 8·5 cm in diameter and 5 cm deep each containing 200 ml of filtered pond water were used. A square perspex block grooved at each corner to hold four cover-glasses in an almost vertical position was placed in each dish. This arrangement was used to hinder the worms from crawling over the cover-glasses. To simplify counting, five *Urceolaria* were brushed from infested '*tenuis-hepta*' into a drop of water on each of four cover-glasses and the latter fixed in the holder. Five cleaned specimens of each host species equivalent in size were immediately added. The number of *Urceolaria* attaching after a given time interval was counted. Two short (15 min and 30 min) and two longer (2 h and 4 h) time intervals were used to afford a measure of any redispersal, because initially it seemed possible that *Urceolaria* may attach only temporarily. However, later work has shown that once attachment has occurred the epizoite usually remains for at least a period of several hours. The experiment was repeated five times for each time interval and the results are recorded in Table 4.

The individual experiments show that occasionally a large majority of *Urceolaria* attaches to one or other of the host species. This must be partly due to chance and also perhaps due to prolonged activity by a particular individual flatworm especially in the four-hour experiments. For example the marked disparity in experiments 3 and 5 (4 h) was due to a large number of attachments to three worms. The totalled values, which would tend to eliminate such chance results, show clearly that the two hosts are equally attractive to free-swimming *Urceolaria*.

This is very apparent in the grand totals which show that out of 157 *Urceolaria* attaching, 76 (48%) did so to *nigra* and 81 (52%) did so to *'tenuis-hepta'*. Table 4 also records that the percentage of free *Urceolaria* which attached during the various time intervals did not increase proportionately with time, mainly, it is believed, because free *Urceolaria* become progressively inactive.

Table 4. *Attractiveness of* Polycelis nigra *and* P. 'tenuis-hepta' *to free-swimming* Urceolaria

Time interval	Exp. No.	No. of *Urceolaria* attaching *P. nigra*	No. of *Urceolaria* attaching *P. 'tenuis-hepta'*	Total attached
15 min	1	0	3	
	2	1	1	
	3	2	4	
	4	4	1	
	5	1	1	
	Total	8	10	18
30 min	1	2	1	
	2	1	0	
	3	3	7	
	4	2	0	
	5	4	3	
	Total	12	11	23
120 min	1	2	4	
	2	11	7	
	3	5	1	
	4	5	2	
	5	2	10	
	Total	25	24	49
240 min	1	6	10	
	2	2	3	
	3	12	1	
	4	11	6	
	5	0	16	
	Total	31	36	67
	Grand Total	76	81	157

A simpler technique was used to compare the attractiveness of *P. tenuis* and *P. hepta*; namely to expose simultaneously a similar sized specimen of each host species to *Urceolaria* in 1·5 ml of water contained in a solid watch-glass. The two worms were added together from a spatula and after a period of 10 min the watch-glass was immersed in a dish containing 100 ml of water to terminate the exposure at once. The number of *Urceolaria* attaching was determined immediately, using chromic acid. The experiment was repeated ten times and a total of 100 attachments examined (Table 5). Since there was no significant difference in the numbers which attached to *P. tenuis* and *P. hepta* in any of the individual experiments it is reasonable to conclude that *Urceolaria* showed no preference for either host species.

The behaviour of detached *Urceolaria* when exposed to hosts could be followed comfortably under a binocular microscope. The peritrichs are quite active at first and move short distances in a linear direction with the aboral surface in front, turning simultaneously in an anti-clockwise direction around the antero-posterior axis when viewed from the aboral surface. They are constantly attaching and reattaching to either the substratum or the water surface. After 15 min or so

activity gradually dies down and less movement occurs. The behaviour of *Urceolaria* when near to *P. nigra*, *P. tenuis* and *P. hepta* is similar and the following activities have been noted on several occasions. The peritrich has been observed to change direction suddenly towards a moving worm when within 1-3 mm of it and attach itself. Sometimes the change may be through 90°. Acceleration of movement by *Urceolaria* sometimes accompanies changed direction. Attachment frequently follows what appears to be chance collisions between *Urceolaria* and an inactive host; similarly when a moving host has crawled over a stationary epizoite.

Table 5. *Attractiveness of free-swimming* Urceolaria *to* Polycelis tenuis *and* P. hepta

Experiment	Attachments		χ^2
	P. tenuis	*P. hepta*	
1	8	9	0·59
2	1	2	0·33
3	6	5	0·09
4	3	4	0·14
5	8	7	0·07
6	1	1	0
7	3	0	3·00
8	3	3	0
9	5	12	2·88
10	9	10	0·05
Total	47	53	0·36

($n = 1$, $\chi^2 = 3{\cdot}84$, $P = 0{\cdot}05$)

An inactive host or one performing irregular movements does not induce change of direction by *Urceolaria*. On no occasion has *Urceolaria* been seen to leave these host species within several minutes of attaching. The behaviour of the peritrich when exposed to an unusual triclad, in this instance *Crenobia* (= *Planaria*) *alpina*, is instructive. It reacts similarly to a moving *Crenobia* as to *Polycelis* but following attachment it immediately detaches. On several occasions the same individual *Urceolaria* has been observed to make half a dozen attempts at attachment one after the other but never remaining more than momentarily. Consequently if *Crenobia* is placed in a concentration of epizoites the latter appear to buzz around the moving worm. The attracting stimulus may be explained in one of two ways; *Urceolaria* is attracted either by the characteristic water movement induced by the host or by some chemical diffusing from the host. Unsuitability of the host seems to be detected only after attachment; its nature is not yet understood.

(*b*) *The dispersal rate*

The dispersal rate of *Urceolaria* from *Polycelis* '*tenuis-hepta*' was calculated at 1% of the infesting population per 6 h with host concentrations of the same order as in nature (Reynoldson 1951). Recent experiments (Table 4) suggested a shorter period of free existence, about 3 h. The former is regarded as more realistic in view of the easy access to the host under experimental conditions. The dispersal rate from *P. nigra* has been determined for comparison using a slightly modified technique. Ten infested *nigra* were kept in 200 ml of filtered pond water in Pyrex dishes 8·5 cm in diameter and 5 cm deep at 20° C in the dark for 24 h. After this

interval the worms were carefully removed and replaced by ten cleaned *'tenuis-hepta'*. The cleaned hosts were then examined for *Urceolaria* after 8 h. Such a recovery method has proved to be more efficient than direct examination of the water; after 8 h about 80-90% of the free *Urceolaria* have attached. As a check on the previous results the experiments were repeated for *'tenuis-hepta'* but after seven tests they were discontinued because it was clear that a rate of 1% (actually 1·13%) was again being obtained. The experiment was

Table 6. *Dispersal rates of* Urceolaria *from* Polycelis nigra *and* P. 'tenuis-hepta'

Experiment Number	Total *Urceolaria* on infested worms		Total *Urceolaria* recovered		% *Urceolaria* dispersing	
	P. nigra	*P. 'tenuis-hepta'*	*P. nigra*	*P. 'tenuis-hepta'*	*P. nigra*	*P. 'tenuis-hepta'*
1	49	367	4	1	8·2	0·3
2	91	354	5	9	5·5	2·5
3	114	479	2	2	1·8	0·4
4	134	405	2	7	1·5	1·7
5	52	245	1	1	2·0	0·4
6	40	248	6	3	15·0	1·2
7	73	355	4	5	5·5	1·4
8	19	—	2	—	10·5	—
9	57	—	0	—	0	—

repeated nine times for *P. nigra*. Both series of results are recorded in Table 6. The dispersal rate from *nigra* showed a wider range of values (0-15%) than from *'tenuis-hepta'* (0-2·5%) which might be expected in view of the low infestations of *nigra*. The average values are 5·5% from *nigra* and 1·01% from *'tenuis-hepta'*. A *'t'* test showed these values to differ significantly ($t = 2{\cdot}330$, $0{\cdot}02 < P < 0{\cdot}05$). Put in a different form, this means that on average an *Urceolaria* living on *P. nigra* spends five hours out of every hundred away from its host; while on *P. tenuis* or *P. hepta* it spends only one hour away.

(*c*) *The population growth-rate of* Urceolaria

The population growth-rate of *Urceolaria* on *Polycelis nigra* and *P. 'tenuis-hepta'* was determined from unit infestations which were obtained by exposing cleaned hosts to *Urceolaria*. The host was removed after a single attachment which is readily observed under a binocular microscope. The infested hosts were then kept in Pyrex dishes containing 100 ml of water from College Pond at 19° C for one week, two individuals of the same species per vessel. The water in each vessel was changed daily to reduce variations of bacterial content from one vessel to another which may develop in stored water. After seven days the number of *Urceolaria* which had grown from the single individual was determined. Data for thirty worms of each 'species' are recorded in Table 7. The average population of *Urceolaria* on *nigra* was 1·73 (S.E. ±0·430) after one week, on *'tenuis-hepta'* 3·30 (S.E. ±0·516): the difference between the means is significant ($t = 2{\cdot}363$, $P < 0{\cdot}05$). Thus *Urceolaria* was able to maintain a markedly higher population growth-rate on *'tenuis-hepta'* than on *nigra* under the experimental conditions. The contrast

arises mainly from a difference in the mortality rate (in half the experiments *Urceolaria* failed to establish itself on *P. nigra*) rather than a difference in the growth-rate of individuals. If initial establishment on *P. nigra* presents difficulties then the higher dispersal rate of *Urceolaria* from this species (22% of the population per day) may be important in lowering the epizoic population.

Table 7. *The number of* Urceolaria *on* Polycelis 'tenuis-hepta' *and* P. nigra *after seven days at 19° C. starting from unit infestation*

Size-groups	Frequency	
	P. 'tenuis-hepta'	*P. nigra*
0	4	15
1-2	9	7
3-4	10	3
5-6	4	4
7-8	1	0
9	2	1
Average	3·3	1·7

The growth-rates of the two urceolarian populations can be expressed as follows: on *P. nigra* $P_n = P_1 2^{0 \cdot 765t}$, on *'tenuis-hepta'* $P_n = P_1 2^{1 \cdot 722\, t}$, where P_n is the population after time t (weeks) when P_1 represents the initial population.

Ten similar experiments were made at 11° C for each host. In the case of *'tenuis hepta'* as host the average number of *Urceolaria* per worm after seven days was 1·9 corresponding to a growth-rate of $P_n = P_1 2^{0 \cdot 926t}$. With *nigra* the corresponding average value was 0·8 *Urceolaria* per worm, i.e. the population had declined by 25%. Lower growth-rates would be expected at this temperature but it is of interest to observe that under similar conditions *Urceolaria* was able to maintain a positive growth-rate on *'tenuis-hepta'* while it was unable to do so on *nigra*. The absence of *Urceolaria* from *nigra* in a number of Anglesey lakes is noteworthy in this connection. A similar comparison of population growth-rates at 19° C was made between *P. tenuis* and *P. hepta*. An average of ten tests for each species gave populations of 3·1 after one week for *P. tenuis* and 3·5 for *P. hepta*, i.e. the growth-rates were similar for these two species.

DISCUSSION

It is apparent that we are dealing with a single biological race of *Urceolaria mitra* and that the contrast in size of the epizoic populations of *P. tenuis* and *P. hepta* on the one hand and *P. nigra* on the other probably arises from differing physiological properties of the host. It seems unlikely that ecological or behaviouristic contrasts between the hosts are involved. The problem now is to convert values for attractiveness, dispersal, and growth-rate of the epizoite on the two host types into a population picture.

Urceolaria becomes planktonic under natural conditions (Reynoldson 1951) and this is probably the main dispersal mechanism. Although both host types are equally attractive to free-swimming *Urceolaria* such dispersal plays an important

part in 'channelling' the epizoites from one host to another, the 'direction of flow' depending on the ratio of the epizoite densities. Such equality is not to be regarded as a neutral factor in the interaction between the two epizoic populations, although it does perhaps simplify the analysis. Dispersal-rates from *P. 'tenuis-hepta'* and *P. nigra* were determined at approximately 1% and 5·5% per 6 h under the experimental conditions. The data suggested that population density did not influence dispersal-rate but other factors such as temperature may well do so. If this factor alone influenced the population balance, equilibrium would be reached when the *'tenuis-hepta'* epizoic population was equal to 5·5 times the *nigra* population. Further, such an equilibrium point is independent of host ratio (Fig. 2, point *A*). If *x* and *y* represent the *Urceolaria* populations

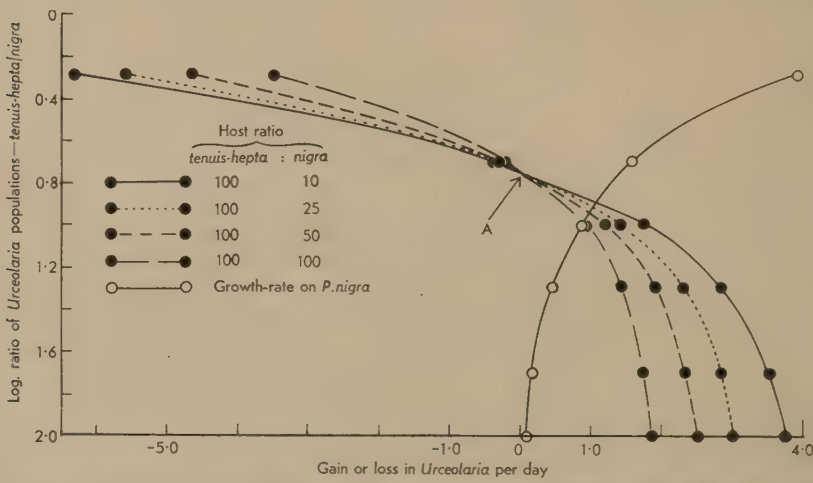

Fig. 2. Comparing the gain (or loss) to the urceolarian population of *Polycelis nigra* from growth *in situ* and dispersal in the presence of *P. 'tenuis-hepta'* at selected host and epizoite ratios. Solid circles represent dispersal curves and open circles the growth curve. Based on Table 9.

per worm on *'tenuis-hepta'* and *nigra* respectively then the following changes will occur when attraction and dispersal alone are operating: equilibrium exists when $x = 5{\cdot}5y$; *Urceolaria* moves from *'tenuis-hepta'* to *nigra* when $x > 5{\cdot}5y$, and from *nigra* to *'tenuis-hepta'* when $x < 5{\cdot}5y$. Dispersal is a factor which persistently tends to bring about equilibrium between the two epizoic populations. Reference to Tables 2 and 10 shows that usually in the field the ratios of the two epizoic populations are such that $x > 5.5y$, indicating the presence of a disruptive factor which prevents the establishment of an equilibrium.

Population growth-rates for *Urceolaria* on *nigra* and *'tenuis-hepta'* have been determined at 19° C under laboratory conditions according to the formulae $P_n = P_1 2^{0{\cdot}765t}$ and $P_n = P_1 2^{1{\cdot}722t}$ respectively (where P_1 = initial population, t = time in weeks). Analysis of weekly growth-rates under natural conditions in College Pond during 1946-47 (Reynoldson 1950) showed a maximum value of $1{\cdot}585t$

compared with $1{\cdot}722t$ under experimental conditions. It is probable that growth-rates comparable to those obtained experimentally do occur in nature but it is evident that the latter is to be regarded as maximal for natural conditions. This may be due to the experimental condition of growth commencing from a single individual, but it also certainly results from the high temperature of cultivation which was unavoidable at the time. The temperature of the natural habitat lies within the range 5-16° C based on a weekly average. It is noteworthy, however, that under laboratory conditions a value of $1{\cdot}722t$ can be exceeded (Table 3). It is not so apparent that the growth-rate of *Urceolaria* on *P. nigra* is maximal because the epizoite often occurs singly on a host in the field. But it is probable in view of the high cultivation temperature that the experimental growth-rate was high compared with natural conditions. This conclusion is relevant when a comparison of the contribution of growth and dispersal towards the *P. nigra* population of *Urceolaria* is considered. The growth of the urceolarian populations based on the experimental rates is shown in Table 8. Clearly such a divergent rate

Table 8. *Population growth of* Urceolaria *on* Polycelis nigra *and* P. tenuis (*or* P. hepta) *at 19° C based on laboratory determined constants*

Week	*P. nigra*	*P. tenuis*
1	2	3
2	3	11
4	8	118
6	24	1 288
8	70	14 030
10	201	152 400
12	579	1 660 000

is a major factor promoting dissimilarity of the epizoic populations on the two hosts. The extent of the dissimilarity produced will depend on the level at which environmental conditions prevent further growth, or to put it another way, on the duration of a particular growth-rate. Thus attractiveness, dispersal and population growth-rate when acting together would usually tend to promote a ratio of the two epizoic populations such that $x > 5{\cdot}5y$ and would account for the ratios of this order found in nature. Furthermore, the ratio will tend to alter continuously depending on the growth- and mortality-rates of *Urceolaria* particularly on *P. tenuis* and *P. hepta*. Such a continual change has been verified under natural conditions (Table 10). It is interesting to note in this connection that when *Urceolaria* was maintained with both host types under more simplified conditions an equilibrium seemed to be established. The data in Table 3 show that under the experimental set-up the ratios of the average urceolarian populations infesting the two hosts were similar in both series, viz. '*tenuis-hepta*' : *nigra* population was 9·03 and 8·97 (Table 3).

A further problem concerns the relative contributions of growth and dispersal to the *Polycelis nigra* population. These depend on a number of factors such as conditions for growth on *P. nigra*, the ratio of the two epizoic populations and the host ratio, all of which are changing continuously. Using dispersal-rates and growth-rates already determined, the relative contribution of each to the *P. nigra* population

has been calculated at static intervals with various ratios of both the epizoic and host populations to cover most natural conditions. The approximate net gain per day to the *P. nigra* epizoic population from dispersal has been calculated according to the formula:

$$\frac{4\,x.X+22y.Y}{100(X+Y)} - \frac{22y}{100}$$ where

x = *Urceolaria* population per worm on *P. 'tenuis-hepta'*.
X = host population of *P. 'tenuis-hepta'*.
y = *Urceolaria* population per worm on *P. nigra*.
Y = host population of *P. nigra*.

The net gain per day from growth has been calculated as equal to $y.(2^{0\cdot765t}-1)$ where t equals one seventh (one day). The results are set out in Table 9 and Fig. 2. For selected host ratios of 1 : 1, 2 : 1, 4 : 1 and 10 : 1 dispersal and growth are equivalent at the following urceolarian ratios of the *'tenuis-hepta'* and *nigra* populations respectively: 9·40, 8·43, 7·94 and 7·65 (Fig. 2, where the growth curve crosses the dispersal curves). When the epizoite ratios are greater, dispersal from *'tenuis-hepta'* contributes more to the *nigra* population, and when less, growth on *nigra* is the more important.

Table 9. *The contributions of growth and dispersal to the urceolarian population of* Polycelis nigra *for varying ratios of host and epizoites. Calculations are based on the number of* Urceolaria *recorded for* P. nigra *in col. 1*

Ratio of *Urceolaria* populations *'tenuis-hepta'* : *nigra*	Net growth of *Urceolaria* on *nigra* per day	Net gain from disperal per day Host ratio *'tenuis-hepta'* : *nigra*			
		1 : 1	2 : 1	4 : 1	10 : 1
100 : 50	3·90	−3·50	−4·67	−5·60	−6·31
100 : 20	1·56	−0·20	−0·27	−0·32	−0·36
100 : 10	0·88	+0·90	+1·20	+1·44	+1·78
100 : 5	0·44	+1·45	+1·93	+2·32	+2·87
100 : 2	0·18	+1·78	+2·37	+2·85	+3·53
100 : 1	0·08	+1·89	+2·52	+3·02	+3·74

The data for Vaynol (Table 10) have been examined in this way to determine at instantaneous points which of the two contributions to the *nigra* urceolarian population was the greater under natural conditions. The calculations have been based on a host ratio for *'tenuis-hepta'* : *nigra* of 10 : 1 (Reynoldson 1955) and on growth- and dispersal-rates as determined experimentally. It has already been shown that the growth-rate used is probably near maximal, and therefore this factor is given more weight than it ought. The results recorded in Table 10 show that dispersal from *'tenuis-hepta'* contributes much more to the *nigra* population than growth; this is particularly apparent in the last column. The picture which emerges from the analysis is that under natural conditions the *nigra* population of *Urceolaria* is determined for the most part by dispersal from the *'tenuis-hepta'* epizoic population, though there may be short intervals when growth on *nigra* dominates. Since the dispersal factor is determined by the growth-rate of *Urceolaria* on *'tenuis-hepta'* this means that the epizoic fluctuations on *nigra* should follow those on

'tenuis-hepta' with a slight lag. Fig. 1 suggests that this is so and it may be concluded that the correlation shown to exist between the two populations resulted mainly from dispersal effects rather than similarity in growth. It also follows that the presence of *P. tenuis* and *P. hepta* will increase the urceolarian population of *P. nigra*. This conclusion has been tested experimentally in an empirical way by comparing initially equivalent epizoic populations of *P. nigra* after one of them had been exposed to infested *P. 'tenuis-hepta'*. In detail, fifteen and ten *P. nigra* respec-

Table 10. *The estimated contribution to the urceolarian population of* Polycelis nigra *by growth* in situ *and dispersal from* 'tenuis-hepta' *based on samples from Vaynol Pond during* 1948. *Gains are expressed as* Urceolaria *per host per day*

Sampling date	*Urceolaria*/ worm		*Urceolaria* ratio	Gain from dispersal	Gain from growth	Gain ratio dispersal : growth
	't.-hepta'	*nigra*	*'t.-hepta' : nigra*			
27 May	35·0	3·0	11·7	0·67	0·23	2·9
30 May	43·3	2·7	16·0	1·04	0·21	5·0
10 June	21·7	0·6	36·1	0·67	0·05	13·4
16 June	34·0	2·5	13·6	0·74	0·20	3·7
24 June	46·0	1·5	30·7	1·37	0·12	11·4
1 July	54·4	1·3	41·9	1·72	0·10	17·2
7 July	74·1	3·8	19·5	1·91	0·30	6·4
15 July	52·9	4·0	13·2	1·12	0·31	3·6
22 July	30·3	3·3	9·2	0·44	0·26	1·7
29 July	20·8	2·0	10·4	0·36	0·16	2·3
5 Aug.	100·4	4·5	22·3	2·75	0·35	7·9
12 Aug.	97·0	6·1	15·9	2·31	0·48	4·8

tively, carrying equal populations of *Urceolaria* were kept in 150 ml of pond water in Pyrex dishes and to the latter were added five infested *'tenuis-hepta'*. To help maintain equivalent bacterial populations the water was changed daily using College pond water. After nine days at an average temperature of 13·6° C the urceolarian populations of the two sets of *nigra* were determined and also those of the *'tenuis-hepta'*. The experiment was set up in duplicate and the results are recorded in Table 11. In each case the *nigra* population of *Urceolaria* exposed to *'tenuis-hepta'* was significantly greater than that of the controls (a *'t'* test gave $P > 0{\cdot}01$ and $< 0{\cdot}05$) thus confirming calculations based on earlier results. On the other hand the two populations under comparable conditions did not differ significantly. No growth occurred in the urceolarian populations of the control *P. nigra*. In the absence of data for the initial epizoic populations of *'tenuis-hepta'* it is not possible to calculate accurately the dispersal-rates necessary to bring about the observed increase in the *nigra* epizoic population. However, in view of the high epizoic population of *'tenuis-hepta'* observed approximately before the experiment and accurately at the end, it is probable that little change took place. On this assumption dispersal-rates close to the previously observed 1% from *'tenuis-hepta'* and 5·5% from *nigra* must have operated, confirming under more complicated conditions the earlier results.

Some of the latest work on host-specificity is that of Davenport (1953*a*, 1953*b*) on commensal polychaetes. He has shown that the commensal reacts positively to

some chemical attractant produced by its host. There are however field observations on these relationships which cannot be explained at present on the basis of his experiments. In this connection it should be recognized that final establishment depends on three stages; contact with the host, maintenance of this contact, and finally ability to grow *in situ*. Davenport's work so far has dealt with the first stage.

Table 11. *Urceolarian populations of* Polycelis nigra *after nine days in the presence and absence of infested* P. 'tenuis-hepta'.

Conditions	Experiment	Average number *Urceolaria* per worm on		
		nigra		*'tenuis-hepta'*
		Beginning	End	End
15 *nigra*	1	3·2	3·3	—
15 *nigra*	2	3·3	3·3	—
10 *nigra* + 5 *'tenuis-hepta'*	1	3·1	8·6	87
5 *'tenuis-hepta'*	2	3·0	11·7	129

Discrepancies between field and experimental observation in the case of these polychaetes may be due to failure on the commensal's part at stage two or stage three. Ideally, in many problems of host specificity the population should form one of the units of study. This approach is one of the important advantages which the use of micro-organisms affords; for a number of reasons it may be difficult with the larger Metazoa.

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SUMMARY

1. *Urceolaria mitra* (von Sieb.) is a common epizoic peritrich of freshwater triclads, particularly the genus *Polycelis*. In nature it always occurs in much larger numbers on *Polycelis tenuis* Ijima and *P. hepta* E. H- & Y. Melander than on *P. nigra* (Müll.); this paper deals with the causes at an ecological level.

2. There is no morphological distinction between the peritrichs from the three hosts and experiments show that irrespective of origin *Urceolaria* always produces a bigger population on *Polycelis tenuis* and *P. hepta* proving that biological races are not involved.

3. The establishment of an epizoic population was examined at three stages; attachment, growth and dispersal. All three hosts are equally attractive to free *Urceolaria*. The growth-rate is much higher on *Polycelis tenuis* and *P. hepta* than on *P. nigra*, while dispersal is much more frequent from *P. nigra*.

4. The larger populations of *P. tenuis* and *P. hepta* are attributed to this higher growth-rate; the reasons for it are not yet known.

5. The urceolarian populations of *Polycelis tenuis* and *P. hepta* are usually so much larger than those of *P. nigra* that the epizoic population of the latter gains from dispersal activities despite the relatively greater dispersal-rate from it.

6. Comparison of dispersal- and growth-rates suggests that the urceolarian population of *Polycelis nigra* is derived mainly from individuals dispersing from *P. tenuis* and *P. hepta* rather than from growth *in situ*. This was confirmed experimentally.

7. Nevertheless, *Urceolaria* can persist on *Polycelis nigra* in the absence of the other two hosts but usually at a low density.

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THE EUROPEAN FLAT OYSTER, *OSTREA EDULIS* L., AS A HOST FOR *MYTILICOLA INTESTINALIS* STEUER

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Baird, Bolster & Cole (1951) reported the occurrence of *Mytilicola intestinalis* Steuer in oysters from the Penryn River, Cornwall, and from the River Blackwater, Essex. So far as is known this was the first time this host-parasite relation had been observed, although in 1946 Odlaug had reported the occurrence of *Mytilicola orientalis* Mori from *Ostrea lurida* Carpenter on the American Pacific coast. Since then infection of a number of molluscs, including oysters, with *Mytilicola intestinalis* larvae has been achieved under laboratory conditions (Hepper 1953). Since *Mytilicola intestinalis* has been shown by Cole & Savage (1951), Korringa (1951, 1953, 1954), and others, to cause a serious loss of condition in mussels, *Mytilus edulis* L., and Odlaug (1946) has concluded that *Mytilicola orientalis* causes loss of condition in *Ostrea lurida*, it may be assumed that any widespread and heavy infection of oysters by *Mytilicola intestinalis* would have serious consequences for the British oyster industry. If the oyster is susceptible to heavy infection this could easily occur, as the mussels in the region of all the major oysterages are already heavily infected with *Mytilicola*. Another disturbing possibility is that if oysters infected with *Mytilicola* were relaid near mussel beds free from the parasite, this could, and in fact almost certainly would, introduce the parasite to the mussel beds, possibly with disastrous consequences. Should this happen in, say, the Wash or North Wales the effect on the British mussel industry would be serious. With a view to investigating these possibilities a survey was made in 1954-55 of the degree to which oysters from various parts of Britain were infected with *Mytilicola*. Some results obtained in 1953 are also included. Samples of twenty oysters each from the Yealm, Crouch, Helford and Fal estuaries had been examined in 1952, but *Mytilicola* was not found. It is considered now that these samples were too small to show the degree of infection and they are not included.

A sample normally consisted of about fifty-sixty oysters, but in some cases it was not possible to get so many, particularly in earlier surveys. The oysters were opened by severing the adductor muscle, followed by removal of the flat valve; the digestive gland and gonad were then carefully sliced away with a sharp scalpel until the gut was exposed. The gut was opened with a needle, thus exposing any parasites present. In practice this is a simple operation, and the parasites, being bright red, show up very clearly; it is unlikely that any were missed, except perhaps a few very early stages. Since this investigation was concerned with established infections, this slight loss, if it occurred, was unimportant.

OBSERVATIONS

Observations are recorded in Table 1. For comparison, the results of Baird, Bolster & Cole are included. Figures for the level of infection of mussels from sites near those from which the oysters were collected are also given; in all cases the samples were of twenty mussels. It will be noticed that of three sites for which

Table 1. *Level of infection of oysters and mussels by* Mytilicola

		Oysters					Mussels	
		Number in sample	Number infected	Total parasites	Maximum parasites per oyster	% infection	Average parasites per mussel	% infection
Penryn R.*	June 1951	116	4	10	3	3·4	2·8	80
R. Blackwater*	July 1951	111	6	7	2	5·4	—	—
R. Blackwater	July 1954	60	3	4	2	5·0	—	—
R. Tamar	July 1953	37	2	8	4	5·4	5·3	80
R. Tamar and R. Lynher	Dec. 1954	21	2	2	1	9·5	—	—
R. Roach	July 1954	51	2	2	1	3·9	1·5	50
R. Roach	Jan. 1955	50	2	3	2	4·0	—	—
Helford R.	July 1954	50	1	1	1	2·0	6·3	100
Milford Haven	Nov. 1954	60†	0	0	0	—	6·3-8·5	85-100
Poole Harbour	Feb. 1955	50	1	1	1	2·0	7·0	100
Whitstable	Jan. 1955	53	1	1	1	1·9	11·8	100

* From Baird *et al.* (1951).

†Milford Haven oysters were relaid in May 1954 from the Menai Straits, where *Mytilicola* does not occur.

comparative figures are available two, the Rivers Blackwater and Roach, show no appreciable change in level of infection during the time elapsing between the taking of the two samples, while the remaining one, from the River Tamar, shows a considerable rise in parasitization. This rise may have been due to the unavoidable inclusion of some River Lynher oysters in the second sample from this area, or to the small size of the second sample. On the whole, however, it does not appear that there has been a general rise in the level of infection in oysters since 1951. Nor does this level appear to vary appreciably throughout the country. It will also be noticed that the level of infection in oysters never approaches that in mussels taken from the same grounds. Many of the infected oysters contained only one parasite, and since fertilization is internal they would be unable to reproduce; these must be considered to be unsuccessful parasitizations. When an opportunity arose, other shellfish living alongside oysters were examined for the presence of *Mytilicola*. At Poole in July 1953, of twenty specimens of *Paphia decussata* L. examined, two were found to contain one specimen each of an early parasitic stage of *Mytilicola*. A large sample of *Paphia aurea* Gmel., a smaller form, from the River Roach, contained no *Mytilicola*.

DISCUSSION

In comparative infection experiments in which mussels and oysters were placed in an aquarium tank of seawater and the infective stages of *Mytilicola* added, the mussels became infected but not the oysters. This was observed by Bolster (1954),

and confirmed by the present author. In a similar experiment using oysters alone (Hepper 1953) infection of these hosts was easily achieved. These experiments and the field observations reported above suggest that oysters are an acceptable host for *Mytilicola* only when mussels are not readily available. It would appear that under present circumstances oysters are only liable to become heavily infected with *Mytilicola* when there are large quantities of larval parasites present and few mussels nearby. This is a situation which is unlikely to occur often in nature since the only source of large quantities of larval parasites would be mussels which would themselves be available for reinfection and would be more 'attractive' than oysters.

Why *Mytilicola* does not infect oysters readily is not known, and it is possible that a strain of parasite may develop which will be more successful. Alternatively, and more probably, this might be brought about by a change in environmental conditions. Bolster (1954) and Hepper (1955) have shown that ecological and environmental factors play a large part in governing the level of infection in mussels. The same is almost certainly true of oysters but the low general level of parasitization renders investigation difficult. It was observed that the female parasites recovered from oysters frequently carried egg sacs, and all attempts to hatch the eggs from these sacs were successful. Bolster (1954) infected mussels with larvae hatched from such eggs. This demonstrates that in the event of infected oysters being relaid near uninfected mussel beds the danger of the latter becoming infected is very real indeed. It is not yet known whether such larvae will infect oysters more readily than larvae obtained from mussels; there does not seem to be any reason for supposing that this would be so.

In view of the fact that *Mytilicola* can infect cockles (Hepper 1953) and *Paphia decussata*, there seems to be no reason why these and possibly other large shellfish should not, in suitable conditions, form further reservoirs of parasites to spread infection. *Mytilicola porrecta* Humes has been found in *Modiolus demissus* Sowerby, *Mytilus recurvus* Raf. and *Venus mercenaria* L. (Humes 1954) and *Mytilicola orientalis* Mori (Odlaug 1946) has been found occurring naturally in a number of hosts including *Crepidula fornicata*, the American slipper limpet. The last-named species was artificially infected with *Mytilicola intestinalis* in the laboratory (Hepper 1953). As it is commonly found in large numbers in the vicinity of oyster beds, *Crepidula* could possibly act as a source of infection; however, no natural infection of *Crepidula* by *Mytilicola intestinalis* has so far been recorded.

SUMMARY

1. *Mytilicola intestinalis* is reported from oysters on the south-west and south-east coasts of Britain, with a level of infection up to 9·5% and 1-4 parasites per oyster. It is also reported for the first time from *Paphia decussata*.

2. It is concluded that *Mytilicola* does not readily infect oysters in the presence of mussels and is unlikely to become epidemic in oysters except as a result of adaptation or a change in environmental conditions.

3. Attention is drawn to the undesirability of relaying infected oysters in the neighbourhood of uninfected mussel beds.

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AN ECOLOGICAL STUDY OF BRACKISH WATER CILIATES

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(With 1 Figure in the Text)

The conditions affecting ciliate Protozoa living in the brackish tide pools of salt marshes offer interesting problems for investigation. Kahl (1933) has published an extensive study of the systematics and distribution of brackish-water Ciliophora, together with some observations on their physiology and mode of life. Kirby (1934) has described a few species from American salt marshes. There appears to be no previous account of British estuarine Ciliophora.

A preliminary survey has been carried out on the salt marshes of the Dee estuary at Parkgate, Cheshire. The aim of the investigation was to record the ciliate species occurring and the nature of the micro-communities in which they exist; to discover how far their distribution was limited by environmental conditions; and to investigate any particular features of their physiology or behaviour which could be related to the exigencies of their environment.

THE HABITAT AND COLLECTING STATIONS

Stopford (1951) gives an historical and general account of the estuary, together with a survey of the metazoan fauna. At Parkgate, which is situated about $8\frac{1}{2}$ miles from the mouth of the estuary, there is an expanse of saltings and mud flats exposed at low tide with a characteristic salt marsh flora (Fig. 1). Plant colonization is extending rapidly, converting the bare mud and sand nearer mid-estuary into saltings, in the typical manner described by Hartley and Spooner (1938). Erosion of the fringe of the saltings has formed a low 'salting cliff' separating them from the flats. The saltings and highest reaches of the flats support a closed plant community dominated by *Festuca rubra* L. The lower flats are partially colonized by vegetation with dominant *Puccinellia maritima* Huds merging into a scattered population of *Salicornia stricta* Moss on the outer sandy fringe.

There are numerous small pools on the saltings and a series of drainage runnels, some of which are continuous with field drains and rivulets on the banks. The tide pools of the flats vary from more permanent ones banked by mud and plants and situated just below the saltings, to temporary pools which evaporate rapidly at low tide. The main channel draining the flats contains several pools of up to 3 ft. in depth. At neaps, these pools may persist when the rest of the channel is dry.

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The channel joins a subsidiary channel of the river, several feet wide, which flows across the sand at some distance from the mudflats. A broad mud path runs from the sea wall across the saltings and flats towards mid-estuary.

The substratum of the saltings and higher reaches of the flats consists of a fine, alluvial mud deposited by the tide. The flats graduate from mud through muddy sand to almost pure sand in the *Salicornia* fringe and beyond it. Stopford (1951) found that the silt content in the upper layers of mud was much greater at neap tides, when the flow of water over the mud was gentle, than at spring tides, when there is more turbulence.

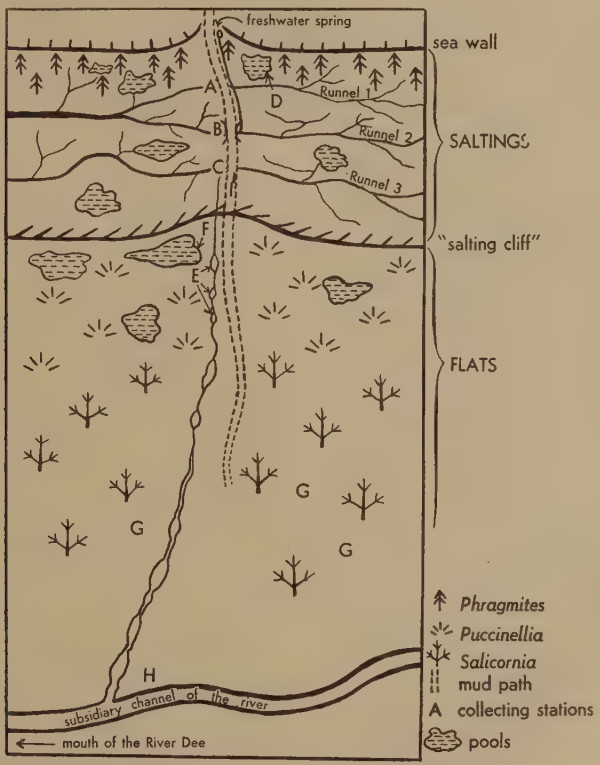

Fig. 1. Sketch map of a section of the Parkgate marshes to show the positions of collecting stations.

The upper margins of the saltings correspond with the level of HWS tides. The salting cliff approximately coincides with the level of MHW, which flood the low-lying reaches of the path, the runnels and those pools connected with them. At neap tides, the saltings are exposed for several days and the higher reaches of the flats also remain exposed occasionally. Pools in these regions may evaporate completely and be refilled with rainwater instead of seawater. The estuary is very shallow; flow and ebb together over the marshes take about 3 h so that there is a very long period of intertidal exposure.

Eleven collecting stations were selected at various points down the shore in pools, runnels, the drainage channel and on the path and mudflats, attempting to include the whole range of possible ciliate habitats. Material from stations A, B and E (Fig. 1) was studied most intensively, as these situations usually contained the most varied ciliate fauna. In dry weather, all stations except A, B, C and E may dry up completely; at such times, collections could only be made from these four stations. Occasional examinations were made of samples from uncolonized sand.

METHODS

From May 1949 to February 1951 material was collected at approximately monthly intervals and more frequently during the summer months. The coloured surface films were scraped up from the mud and placed in clean, screw-capped jars together with a water sample. In the laboratory the samples were tipped out into small, shallow dishes with covers, with only a thin layer of sample water over the mud. The surface film, which disintegrated during collection and transport, reforms within a few hours especially if the dishes are placed near a window. Part of the water samples were used for salinity determinations.

The material was examined as soon as possible after collection, usually within 24 hr. After longer periods, faunistic changes are rapid and largely unpredictable in material maintained in the laboratory. The necessity for rapid examination implies the recording of those species present in sufficient numbers to be apparent with careful observation; it is unlikely that species present as rare, scattered individuals will be recorded. Several small samples were removed from each gross sample and examined microscopically. One method of examination consisted of placing a clean coverslip in contact with the surface film. After about an hour, many strongly thigmotactic forms have adhered to the coverslip which may then be removed and examined. Larger ciliates and weakly thigmotactic species are not recorded by this method, however.

A qualitative survey of the Ciliophora was made. The relative abundance of species was estimated very roughly and it is indicated by arbitrary terms (Tables 3 and 4). Counts of individuals occurring are of no value unless adequate methods of obtaining uniform samples both in the field and in the laboratory can be devised. In practice, it is almost impossible to attain these desiderata. The nature of the associations of micro-organisms is the chief obstacle to accurate sampling. Local aggregations of food organisms lead to restriction of the consumers of such food into areas of microscopic dimensions. Interpretation of single samples is thus made difficult, while the danger of obliterating the behaviour of the animals by averaging results from a number of samples is apparent. Furthermore, the relatively enormous day-to-day fluctuations occurring in the microcommunities demand counts at very frequent intervals if they are to be of any value. In view of these considerations, it seems that the empirical methods utilized in the present work provide an adequate foundation for the generalized conclusions made regarding the distribution of the marsh Ciliophora.

ENVIRONMENTAL CONDITIONS

(*a*) *Temperature*

The maximum daytime temperature of 28° C was recorded for station F (8 June 1950). The minimum daytime temperature recorded was 3·5° C at station C in December 1949. A maximum and minimum thermometer was placed in station C for a month between 21 Nov. and 20 Dec. 1950. The minimum temperature recorded during this period was −3·3° C and the maximum was 10° C. The total variations in temperature (Table 1) therefore cover almost the whole range over

Table 1. *The ranges of temperature, salinity, and hydrogen-ion concentration*

	Station	Temperature (°C)	Salinity (‰)	pH	
15 Nov. 1949	A	8·5	20·6	8·2	ELWN; good growth of diatoms everywhere
	B	8·5	22·8	8·0	
	E	8·0	29·2	8·2	
20 Dec. 1949	A	4·0	16·7	7·9	2 h after HW; poor growth of diatoms
	B	4·0	15·9	7·9	
	C	3·5	17·5	7·7	
	E	4·0	—	7·7	
10 Jan. 1950	A	9·5	12·2	—	LW
	B	9·5	17·9	7·4	
	C	9·5	—	7·3	
	E	9·5	—	7·7	
20 Feb. 1950	A	7·5	22·3	7·8	HW
	I	7·5	22·3	7·8	
14 March 1950	A	6·5	16·3	7·6	LW
	B	6·5	19·3	7·6	
	D	6·5	19·0	7·6	
	E	6·0	—	8·2	
	F	5·5	—	8·2	
10 May 1950	A	16·5	14·8	8·0	ELWN; fairly good growth of diatoms everywhere
	B	18·0	19·2	8·3	
	C	16·5	20·8	8·3	
	E	20·0	16·9	—	
8 June 1950	F	28·0	30·8	—	Very hot dry weather
	G	28·0	31·1	—	
13 Aug. 1950	A	19·5	13·6	8·0	LWN; all other stations completely dry; poor growth of diatoms everywhere
	B	19·0	20·7	8·2	
	C	21·0	17·8	8·0	
	E	21·0	26·9	8·2	
	H	20·5	22·8	8·3	
20 Dec. 1950	A	4·5	11·2	—	Thaw following several days of snow
	B	4·5	12·4	—	
	C	5·0	12·5	—	
	E	4·5	19·5	—	
	F	4·0	8·6	—	
	I	—	2·2	—	

which the ciliates are capable of normal activity. Methods of survival during extremely low temperatures are unknown; the wide range of forms occurring on 20 December 1950 (Table 2) after extrenely cold weather indicated that the ciliates can survive such cold conditions. Cysts of some species may be able to withstand freezing.

The ciliates are usually more abundant at high temperatures; perhaps the expected correlation between increased metabolic rate and division rate of both

Table 2. *Occurence of ciliates on the Parkgate marshes from May 1949 to April 1951: composite record for all collecting stations*

	10 May 1949	24 June	21 July	28 July	8 Aug.	11 Aug.	17 Aug.	24 Aug.	31 Aug.	20 Sept.	21 Oct.	15 Nov.	20 Dec.	10 Jan. 1950	20 Feb.	14 Mar.	3 May	10 May	8 June	12 July	19 July	30 Aug.	5 Oct.	21 Nov.	20 Dec.	10 Feb. 1951	6 Apr.
Aspidisca cremata Fabre-Domergue	–	·	·	·	·	–	+	·	·	+	+	+	·	+	·	·	+	+	·	·	·	+	+	+	·	+	+
Aspidisca sp.	+	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Blepharisma salvanum Florentin	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Chaenea teres Dujardin	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Chilodon cultumi Kahl	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Chilodontopsis elongata Kahl	·	·	·	+	·	·	·	·	·	+	+	+	+	+	·	+	·	·	+	·	·	+	+	+	+	+	·
Chlamydodon mnemosyne Ehrenburg	+	·	·	·	·	·	·	·	·	·	+	+	+	+	·	·	+	·	·	·	·	+	+	+	·	·	·
C. triquetrus O. F. Müller	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cohnilembus pusillus Quennerstedt	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Condylostoma patens O. F. Müller	–	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
C. patulum Claparède and Lachmann	–	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Coleuronia annulata Stokes	·	·	·	+	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Cryptopharynx setigerus Kahl	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Dileptus sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Disphorys appendiculatus Ehrenburg	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·
D. sculum Dujardin	·	·	+	·	·	·	·	·	·	+	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·
Dysteria sp.	·	·	·	·	·	·	·	·	·	·	+	·	·	+	·	·	·	·	·	+	·	·	·	·	·	·	·
Euchelys pectinata Kahl	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Euplotes charon Stein	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
E. harpa Stein	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Frontonia marina Fabre-Domergue	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Homalozoon caudatus Kahl	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Holophrya sp. (?)	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Holostichia kessleri Wrzesniowski	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Kentrophorus sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Keronopsis rubra Ehrenburg	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lacrymaria coronata Clap. and Lach.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
L. lagenula Clap. and Lach.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
L. olor var. *marina* Kahl	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Loxodes fasciola Wrzesniowski	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
L. folium Dujardin	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Lionotus sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Loxophyllum fusciolatum Kahl	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
L. helus Stokes	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·

L. helus var. multiverrucosum Kahl
L. meleagris Dujardin
L. setigerum Quennerstedt
L. undulatum Sauerbrey
Mesodinium acarus Stein
M. pulex Clap. and Lach.
Micromitra retractilis Clap. and Lach.
Nassula citrea Kahl
Nassula sp.
Opisthotricha parallelis Engelmann
Pleuronema crassum Dujardin
P. marinum Dujardin
Placus socialis Fabre-Domergue
Prorodon discolor Ehrenburg var. marinus Kahl
Spirostomum teres Clap. and Lach.
S. loxodes Stokes
Strombidium elegans Florentin
S. stylifernm Levander
Strombidium sp.
Stylomethes sp.
Stylonychia pustulata Ehrenburg
Trachelocerca fusca Kahl
T. phoenicopterus Cohn
T. subviridis Sauerbrey
Uronychia transfuga O. F. Müller
Vorticella microstoma Ehrenburg
Vorticella sp.

ciliates and their food supply is indicated, but the relationship has not been investigated. At the same time, some species may be abundant at low temperatures, notably *Strombidium elegans* which was often superabundant at temperatures between 4·5° and 7·0° C. In general temperature variations appear to have little effect upon the occurrence of particular species. One can only conclude that there are no striking variations in population correlated with temperature change.

(*b*) *Salinity*

The salinity of water samples was estimated by titrating with silver nitrate solution, following the method described by Harvey (1945). For small samples, the freezing point was determined using Beckmann's apparatus and the salinity calculated from the value obtained.

Recorded salinities (Table 1) fall mainly within a restricted range between 11 and 23‰ salinity (31% and 65% seawater respectively). The maximum salinity of water carried over the habitats by the flood tide is 22·3‰. The salinity in isolated pools may be greatly increased by evaporation during hot weather. On 8 June 1950, a value of 31·1‰ was recorded for station G, when the temperature of the pool was 28° C. Considerable dilution may be caused by periods of rain or snow; e.g. samples from stations F and I had salinities of 8·6 and 2·2‰ respectively after a period of snow. Many typical species of ciliate were recorded at these low salinities (Table 3). Some of these species also occurred at station F in the highest recorded salinity for the station, 30·8‰ (8 June 1950, Table 3).

Fauré-Fremiet (1950*c*) has shown that in fine sands, very high concentrations of the ionic constituents of seawater are retained by adsorption on the surfaces of particles. The salinity of the water in the interstitial spaces may be as much as 25% higher than that of the overlying water. Stopford (1951) has found that the salinity of the interstitial water in the Dee estuary may be as much as 10-20 % higher than in neighbouring channels at low water, and points out that the salinity of interstitial water, although variable, will change considerably less than the free water above. Evidently, the salinity of the microhabitats is less variable than analysis of the free water suggests and the ciliates will be protected from the low salinities which are lethal to many of them. The records indicate that many of the marsh ciliates can withstand wide variations in the salinity of the external medium. Apparently their distribution is not restricted by local salinity changes.

(*c*) *Hydrogen-ion concentration*

Observations supported the generally accepted conclusion that the actual values determined for hydrogen-ion concentration show little correlation with the distribution of the fauna, and merely serve to indicate underlying chemical change. No attempt has been made to record changes in pH precisely. A few determinations were made using phenol-red as an indicator; the results are given in Table 1. The range of variation is from pH 7·3 to 8·3. Estuarine water carried over the marsh at flood tide has a pH of 7·8. No direct relationship was observed between

hydrogen-ion concentration and either temperature or salinity. Higher temperatures and greater salinities are often accompanied by more alkaline conditions, but there are frequent exceptions to both these generalizations. Biotic changes influence the hydrogen-ion concentration considerably. Photosynthetic activity increases the alkalinity during the daytime (Atkins, 1922*a*, 1922*b*). Conversely, accumulation of respiratory carbon dioxide, and the activities of sulphur bacteria, abundant just below the mud surface, produce more acid conditions.

Table 3. *Protozoa occurring in samples from station F*

\+ = present—one to a few specimens per sample drop.
f = frequent—about ten specimens per sample drop.
a = abundant—between ten and fifty per sample drop.
s = superabundant—over fifty per sample drop.

	10 Jan. 1950	14 Mar. 1950	8 June 1950	21 Nov. 1950	20 Dec. 1950	10 Feb. 1951	6 April 1951
Temperature (°C·)	—	—	28	—	4	—	—
Salinity (‰)	—	—	30·8	—	8·6	—	—
CILIATA							
Aspidisca crenata	.	.	a	+	.	.	+
Chilodon calkinsi	.	.	.	.	.	+	+
Chlamydodon mnemosyne	+	.	.	.	+	.	.
C. triquetrus	.	.	+	f	.	+	+
Cryptopharynx setigerus	.	.	.	+	.	.	.
Diophrys appendiculatus	.	.	+	+	+	+	.
D. scutum	.	+	.	.	.	.	.
Dysteria sp.	.	.	.	.	.	.	+
Euplotes charon	.	+	+	.	+	+	+
E. harpa	.	.	.	+	.	.	.
Frontonia marina	.	.	.	.	+	.	.
Holosticha kessleri	.	a	.	+	f	+	.
Lionotus folium	.	.	.	.	+	.	.
Loxophyllum fasciolatum	.	+	.	.	.	.	.
L. helus	.	.	.	.	+	.	+
L. meleagris	.	.	.	.	.	.	+
L. setigerum	.	.	.	.	+	.	.
Mesodinium acarus	.	.	.	a	.	.	.
M. pulex	.	+	.	.	.	.	.
Micromitra retractilis	.	.	.	.	.	+	.
Opisthotricha parallelis	+	.	.	a	.	+	+
Pleuronema crassum	.	+	.	.	.	+	.
P. marinum	.	.	.	+	.	.	.
Strombidium elegans	a	.	+	+	f	a	f
Trachelocerca phoenicopterus	.	.	+	.	.	.	.
Uronychia transfuga	.	.	.	.	+	.	.
MASTIGOPHORA							
Anisonema acinus	.	.	.	+	.	.	.
Anisonema sp.	.	.	+	.	.	+	.
Euglena limosa	.	+	.	.	.	.	.
E. polymorpha	.	.	.	+	.	.	.
Euglena sp.	.	.	.	a	+	.	.
Oxyrrhis marina	.	+	.	.	.	.	.
Urceolus cyclostomus	.	.	.	+	.	.	.
SARCODINA							
Amoeba verrucosa	.	.	.	+	.	.	.
Cyphoderia ampulla	.	.	.	.	+	.	.

Table 4. *Protozoa occurring in samples from station B*

	10 May 1949	21 July	28 July	8 Aug.	11 Aug.	17 Aug.	24 Aug.	31 Aug.	20 Sept.	21 Oct.	15 Nov.	20 Dec.	10 Jan. 1950	14 Mar.	3 May	10 May	8 June	12 July	19 July	30 Aug.	5 Oct.	21 Nov.	20 Dec.	10 Feb. 1951	6 Apr.
Temperature (°C.)	—	18·5	—	—	15	—	—	—	—	10·5	8·5	4	9·5	6·5	—	18	22	19	—		14	7	4·5	4·5	12
Salinity (‰)	—	—	—	—	—	—	—		20·9	21	22·8	15·9	17·9	19·3	21·3	19·3	19·8	20·7		15·8	17·1	16·8	12·4	16·8	—
CILIATA																									
Commonly occurring:																									
Aspidisca crenata	.	.	.	.	+	.	+	.	.	.	.	.	.	.	a	.	+	+	.	+	+	.	.	+	.
Chilodon calkinsi	.	.	.	.	.	.	.	.	+	.	.	.	.	+	s	s	+	.	.	a	+	.	+	+	.
Chlamydodon mnemosyne	s	.	+	.	s	a	+	+	+	+	+	.	+	.	.	.	.	.	.	.	+	.	.	+	.
C. triquetrus	.	.	.	.	.	.	.	.	.	.	.	.	+	.	a	s	s	+	+	s	a	+	.	+	.
Euplotes charon	+	+	.	.	a	+	a	.	.	.	.	.	.	+	f	.	.	.	.	.	.	.	.	+	.
Frontonia marina	a	.	s	.	a	a	s	.	a	.	+	.	.	.	.	.	.	.	s	.	+	.	.	.	.
Holosticha kessleri	.	.	.	.	+	.	.	.	.	.	.	+	+	+	+	f	.	.	.	+	.	.	+	.	.
Lacrymaria olor var. *marina*	+	+	+	+	+	+	+	.	.	.	.	.	.	+	+	.	.	.	.	a	+	.	.	+	.
Mesodinium acarus	f	+	+	.	+	.	.	.	.	.	+	.	+	.	+	+	.	.	.	.	.	.	+	.	+
Pleuronema marinum	.	a	.	.	+	+	.	.	.	+	.	.	.	.	+	.	+	.	+	+	.	.	+	.	.
Strombidium elegans	f	+	.	+	+	a	+	a	.	+	a	.	+	a	+	+	+	.	a	.	+	s	+	+	s
Trachelocerca phoenicopterus	.	+	.	.	.	.	+	.	.	.	.	.	.	+	.	.	+	.	+	+	+	.	.	.	.
Uronychia transfuga	f	+	+	.	.	+	.	.	+	.	+	.	.	+	.	.	+	.	.	.	.	.	.	.	.
Occasionally occurring:																									
Chilodontopsis elongata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Condylostoma patens	.	.	.	.	.	a	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
C. patulum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.
Cryptopharynx setigerus	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Diophrys appendiculatus	.	.	.	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
D. scutum	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Dysteria sp.	.	+	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euplotes harpa	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Heminotus caudatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Holophrya sp. (?)	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	+	.	.	.	+
Lacrymaria coronata	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	+	.	.
L. lagenula	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lionotus folium	+	.	.	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Loxophyllum helus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	+	+	.	.	.
L. setigerum	.	+	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.

| | | |

Many protozoa are capable of growth over a wide range of pH (Kudo 1946). The estuarine ciliates investigated support this conclusion; possibly more restricted ranges may offer optimal conditions for some species which tolerate a wide range.

RESULTS

Sixty-one species of Ciliophora have been recorded (Table 2). Only the most obvious members of the Mastigophora and Sarcodina have been recorded. All collections usually contain numerous very small dinoflagellates. The smaller flagellates have been ignored altogether. Representative records for two collecting stations are presented (Tables 3 and 4).

(*a*) *Seasonal distribution*

The chief general conclusion which can be drawn from the records is an absence of major qualitative fluctuations in the ciliate populations of the marshes corresponding with gross seasonal changes in the environment. In Table 3 the total collections of ciliates from all stations are summarized for the whole period of examination. No seasonal variation in the total number of species is indicated; summer and winter populations are equally varied. It is also apparent that certain species may occur at all times of the year, and these species include most of the ciliates which are common in individual stations (Table 5). No single species has been recorded in every collection, although *Strombidium elegans* may reasonably be said to be ubiquitous.

Table 5. *Species occurring commonly throughout the year*

Aspidisca crenata	*Holosticha kessleri*	*Mesodinium acarus*
Chlamydodon mnemosyne	*Lacrymaria coronata*	*Opisthotricha parallelis*
C. triquetrus	*L. olor* var. *marina*	*Pleuronema marinum*
Diophrys appendiculatus	*Lionotus folium*	*Strombidium elegans*
Euplotes charon	*Loxophyllum helus*	*Trachelocerca phoenicopterus*
Frontonia marina	*L. setigerum*	*Uronychia transfuga*

A few species are recorded only during certain restricted periods. *Placus socialis* and *Euplotes harpa* have only been found between April and October inclusively. On the other hand *Strombidium styliferum* has never been recorded during the summer months but only between November and May. *Lionotus folium* and *Frontonia marina*, although included in Table 5, show some indications of restricted occurrence. The former appears more constantly during late summer and early winter than during spring and early summer; the latter is rarer during the winter months, but is very abundant during July and August. No conclusions can be drawn about the remaining ciliates in the complete list. Many of them were only recorded once or twice during the whole period of examination. In general, collections between May and September contained greater numbers of ciliates than at other times of the year. This is particularly true of the diatom feeders, *Chlamydodon mnemosyne*, *C. triquetrus*, *Chilodon calkinsi* and *Frontonia marina*.

Incidental observations on the Sarcodina and Mastigophora suggest that those two classes are characterized by abrupt population increases which die down as

quickly as they occur. For example, at station A swarms of an unidentified *Euglena* occurred in July 1950. *Euglena limosa*, although a fairly constant inhabitant in small numbers at all times of the year, appeared in large numbers in January 1950 giving a bright green colour to patches of mud about a foot square. *Anisonema acinus* also shows sudden large increases in numbers, as recorded in November 1950. Wang (1928) reports abrupt transitory maxima in the occurrence of certain freshwater planktonic Mastigophora.

The occurrence of certain Mastigophora may be correlated with organic pollution in some of the habitats. Certain organic compounds facilitate the growth of many green as well as many colourless Euglenidae (Pringsheim 1949). *Euglena limosa* is reported fairly constantly from stations A and B, where there is a high degree of pollution by land drainage. These stations frequently contain flourishing populations of various *Euglena* species together with members of the Anisonemidae Bracher (1929) reports *E. limosa* in a polluted habitat on the banks of the Avon, and Lackey (1938) reports it and also *E. polymorpha* from a polluted stream and from an Imhoff tank.

(*b*) *Distribution down the shore*

There is no clear distinction between the ciliate faunas of the various stations (Fig. 1) from the sea wall out into the estuary. The ciliates included in Table 5 appear from time to time in nearly all the stations. Stations A, B and C and the pools of station E contain the richest ciliate fauna, both qualitatively and quantitatively, at all times of the year; these habitats offer excellent conditions for the aggregation of organic matter and micro-organisms. Protection of a habitat by surrounding banks of soil and pollution by land drainage appear to be two major factors in providing a suitable environment for the establishment of micro-communities. Both these requirements are provided by stations A, B, C and E. By comparison habitats such as stations G and H, in which the substratum is almost unpolluted exposed sand, support a much smaller and less varied association of ciliates.

(*c*) *Predators*

The metazoan microfauna of the marsh habitats includes nematodes which are abundant in all collections, rhabdocoeles and crustaceans which are found fairly frequently, and rotifers and gastrotrichs which occur only rarely. Small annelids and molluscs appear sporadically.

The ciliate populations are apparently little restricted by the attacks of metazoan predators. There appears to be little knowledge of the feeding habits of the nematodes. In laboratory cultures of saltmarsh material, they have been observed feeding on small diatoms and clumps of bacteria, but they have not been observed to feed upon Protozoa. The Crustacea feed on diatoms and green flagellates mostly and this is also true of the rhabdocoeles observed. Rotifers have been observed browsing on swarms of *Euglena* spp. Flagellates, especially Euglenidae, may form a considerable part of the dietary of the smaller Metazoa.

(*d*) *Distribution of the ciliate fauna in relation to the physical nature of the habitat*

The ciliates of Parkgate can be divided into two groups: the sand-dwelling forms, and those which rarely occur in the interstitial spaces but nearly always in association with the algal films which develop at the phase boundaries, particularly at the mud-water interface.

Stopford (1951) found that in all types of substratum at Parkgate, the sand is very fine, generally of less than 0·5 mm. particle size. The majority of the psammophilous ciliates encountered at Parkgate belong to the type described by Fauré-Fremiet (1950*b*, 1950*c*, 1951) as mesoporal, i.e. occurring in sands with a mean particle size of 1·8-0·4 mm. He divides mesoporal species into two groups:

1. Typically sand-dwelling species, of small or medium size, with a characteristic motion alternating between periods of swimming and quiescence in contact with solid surfaces. This type is represented at Parkgate by two species each of *Strombidium* and of *Mesodinium*, and by *Placus socialis*. These species may be taken occasionally in plankton samples from the habitats.
2. A more restricted group of widely distributed forms which frequently occur in mesoporal sand, but which are just as commonly associated with the littoral algal films. Many of the marsh ciliates belong to this category, e.g. *Aspidisca* spp., *Condylostoma patens*, *Diophrys* spp., *Euplotes* spp., *Frontonia marina*, *Lacrymaria* spp., *Lionotus* spp., *Loxophyllum* spp., *Pleuronema* spp., *Uronychia transfuga*.

Fauré-Fremiet describes a second type of psammophilous ciliate as microporal —living in sand of a mean particle size of 0.1 to 0.3 mm. These forms are elongated, thread-like or ribbon-like, often 1-2 mm. long and with strongly thigmotactic ciliation. Fauré-Fremiet divides microporal ciliates into exclusively microporal forms, and euryporal forms which are found in both fine and coarse sands. Of the Parkgate ciliates, euryporal species are *Trachelocerca phoenicopterus*, *T. fusca*, *Holosticha kessleri*, *Condylostoma patulum* and *Micromitra retractilis*. Microporal forms are less common than mesoporal ones, and exclusively microporal ones have not been recorded, with the single exception of *Kentrophorus* sp. Some of the ciliates found at Parkgate are never observed in the interstitial spaces of the sand but are confined to the diatom film; these are usually diatom feeders, e.g. *Chilodon calkinsi*, *Cryptopharynx setigerus*, *Chlamydodon mnemosyne*. They have certain characteristics in common with the sand-dwelling forms, being flattened, often ciliated on the ventral surface only, and strongly thigmotactic. They differ however in seeming to be bound to the diatom film; they do not show periods of free-swimming activity in the bulk of the medium as do many of the mesoporal ciliates.

STRUCTURE OF THE CILIATE COMMUNITIES

The evidence presented in the preceding sections confirms the expectation that the marsh ciliates in general are tolerant of wide variations in temperature, salinity and hydrogen-ion concentration. Their behaviour is not regulated by a seasonal

reproductive cycle. Metazoan predators are few and unimportant. The ciliates which occur abundantly on the mud surface and which appear on casual examination to consist of chance aggregations, provide material for a study of the relationships which maintain them in a balanced community. These ciliates occur in close association with the microflora —— diatoms and other algae which creep over the mud surface, and bacteria which also aggregate in large numbers at the mud-water interface.

(*a*) *Diatoms*

Diatoms occur abundantly in the surface films covering all exposed areas of mud and are also found in smaller numbers collected in the depressions in the sand of the uncolonized littoral. The collecting stations selected support a good growth of diatoms at all times of the year except for stations G and H, where diatom growth is poor and consists mostly of the smaller species. The density of the diatom population is indicated by the colour of the film. Sparse populations give a faint yellow-green colour to the mud surface, and the colour shades through yellowish-brown, brown, dark chocolate brown to almost black, the blackish areas supporting large numbers of diatoms. Stations G and H (Fig. 1) are usually only faintly yellow; stations F and D are usually yellow-green to yellow-brown. At stations A, B, C, E and I, the diatom film is usually a rich brown, but under optimum conditions of illumination and after maximum exposure at low tide it may become almost black.

Aleem (1950) describes the intensity of colour attained by different concentrations of the diatom, *Pleurosigma balticum*, on mudflats at Whitstable. He attributes a faint yellow colour to a population of approximately less than 600 individuals per cm^2, and a blackish colour to a population of approximately 8000 to 9000 per cm^2. As there is a mixed population of diatoms of varying size on the Parkgate mud, Aleem's figures cannot be related directly to the observations made above, but they give an indication of the range of numbers occurring.

More than forty species have been recorded from Parkgate; all are brackish water species and the different collecting stations are characterized by different associations of species, although some species occur in many of the habitats (Dr F. E. Round, unpublished information). There is no definite information about the seasonal fluctuation in numbers, but the diatom populations appear to decrease in winter, when temperature and illumination are low, and to reach a maximum during the summer, when conditions of light and temperature are more favourable. Estuarine conditions favour the aggregation of inorganic nutrients essential for diatom growth. Salts, especially nitrates and phosphates, will be carried into the habitats by land drainage, and the tidal waters will carry a supply of dissolved nutrients acquired by the churning up of the littoral zone. There is usually an abundant supply of essential inorganic nutrients in estuaries (Harvey 1945, Allee *et al.* 1949).

The nature of the habitats promotes the growth and reproduction of diatoms. The colloidal substrate of fine alluvial mud is of major importance to the diatoms

in three ways: by promoting the deposition of nutrients after each tidal disturbance; by maintaining, by its absorptive properties, a dynamic equilibrium of ionic concentration in the interstitial water, thus regulating the supply of available nutrients; and by keeping the subsoil permanently waterlogged, so that the fine particles at the surface maintain a water supply by capillarity and adsorption. On a substratum with a coarser average particle size, the water would drain away too quickly and desiccation would be inevitable. The habitats are also particularly favourable to diatom growth because they are submerged for very short periods, and during the rest of the day the films are covered only by a very thin layer of water, or are uncovered, and thus receive a maximum amount of illumination.

(*b*) *Bacteria*

A sample of material from station B was analysed by the Bacteriological Department of Liverpool University and was found to contain representatives of many of the commonest sewage bacteria as well as many soil forms. In the habitats studied the major source of bacteria is from land drainage. Tidal inundation lasts two to three hours; flow of land drainage is continuous, thus favouring a preponderance of terrigenous and freshwater bacteria. The toxic effects of seawater on non-marine bacteria has frequently been reported (ZoBell 1946) but ZoBell also observed that the dilution of seawater by 50% reduces both its growth-promoting properties for marine bacteria and its toxicity towards terrestrial forms.

The availability of organic compounds is important in determining the bacterial flora of the associations. Accumulation of organic material will depend upon both physical and biotic influences. Some domestic sewage is discharged directly on to the marsh, and much organic material is carried on to the marsh by drainage and seepage. The products of excretion, secretion and decay of micro-organisms will give a rapid turnover of abundant autochthonous organic material providing a variety of substrates for the activities of bacteria. Breakdown of organic compounds to simple ions by bacteria will also supplement the supply of inorganic nutrients.

The physical nature of the habitats selected provides excellent conditions for the aggregation and multiplication of bacteria. Pools and runnels contain a surface layer of sedimentary particles; these include much colloidal material, which is of great importance in localizing the occurrence of bacteria and consequently of associated organisms. Sedimentation tends to segregate particles of similar size, so that many bacteria are thrown down with other particles of colloidal dimensions. Renn (1937) points out that that is a most important way in which bacteria are removed from coastal waters. Furthermore the mixing of freshwater and seawater causes flocculation of suspended matter, which will accelerate sedimentation. Much deposition of suspended matter, including bacteria and organic nutrients, will occur in the runnels and pools after each tide.

(*c*) *Mechanical structure*

The association collecting at the mud-water interface is part of the littoral

microbenthos. The aggregation of the microbenthos occurs partly as a result of the orientations of the organisms themselves, partly as a result of the action of physical forces such as sedimentation, cohesion and surface tension. Similar aggregations of organisms at the water-air interface form the neuston. Both microbenthos and neuston are incorporated into clearly visible films. The microbenthic films vary from yellow to blackish-brown, the colours depending on the presence of diatoms and other algae. The films have coherence and structure, illustrated by the way in which they bind the surface of the mud together, and the fact that they can be lifted in strips from the mud or from the upper water surface with collecting tools. The neustonic films particularly may be lifted in masses which do not readily disintegrate. The coherent properties of the film are largely due to the secretions of the organisms. The diatoms secrete large quantities of mucilage in connection with their mode of locomotion and certain of the free-living bacteria produce polysaccharides of a mucilaginous nature. Many of the Protozoa feeding upon bacteria have been shown to excrete mucus, which effects flocculation of the bacteria (Pillai & Subrahmanyan 1942, Hardin 1943, Watson 1944, 1945). In addition mucus secretion accompanies locomotion in many ciliates (Picken 1937).

In a body of water containing a heterogeneous collection of polluting substances, a surface film will be formed automatically by the accumulation at the surface of materials which tend to lower the surface tension of the liquid. Such hydrophobic material includes bacteria (ZoBell 1946). Proteins, although they are often slightly hydrophilic, tend to form films on water surfaces. Goldacre (1949) has made a study of inland waters of different kinds and finds that they are all characterized by a well-defined surface film consisting of protein or lipoprotein, usually arranged in a monomolecular layer. He stresses the ecological importance of the film to small animals and plants, not only in providing mechanical support, but also as a possible food source. The protein films of brackish or salt water have apparently never been investigated, but it seems possible that the aggregations of protein at the water interfaces may be increased by the salting-out effect of the greater concentrations of ions present in seawater.

A surface film does not form on running water but only on standing pools, most obviously on the leeward edges of the pools when there is any wind. Presumably any organisms present at the surface are blown to the edges, where the wind probably also increases the concentration of organic molecules, the whole collection becoming organized into a film. Sudden gusts cause the film to crinkle into folds which tend to flatten out again when the wind drops, giving another indication of the structural coherence of the film. It may also be formed by the sloughing-off of pieces of the film from the mud-water interface. Gas bubbles, often 1-2 cm in diameter, are sometimes produced beneath the film and finally float it up to the water-air surface.

The neuston usually contains abundant diatoms and bacteria, and often supports as large and varied a protozoan fauna as the mud film itself. The neuston collected from a still pool in early November 1950 contained the following forms:

CILIATA	MASTIGOPHORA
Chlamydodon triquetrus	*Euglena limosa*
Euplotes charon	*Oxyrrhis marina*
Lacrymaria coronata	
Holosticha kessleri	
Loxophyllum helus var. *multiverrucosum*	
Placus socialis	
Uronychia transfuga	

The diatoms and other algae are the most important organisms in forming and maintaining the films. Their activities have been observed by pipetting small quantities of material containing large numbers of diatoms into Petri dishes containing a nutrient solution (the medium described by Mare (1942) modified by using 50% seawater as the basic constituent), in which the diatoms may be cultured for considerable periods. If only a small number of diatoms is inoculated into the dish and dispersed as far as possible, within a few hours they clump together in small nodules which prove to be stellate clusters of pennate diatoms, the individual members of which are in constant motion. When large numbers are present together with some mud, they form aggregates from and to which migrations continually occur. Within a day or two many have migrated out over the bottom of the dish, and there is a visible film formed on the bottom surface. Microscopic examination shows that the film consists of a layer of transparent material with diatoms creeping over it at intervals, and with quantities of bacteria and algae adhering to it. This film has apparently been formed by the secretions of all the organisms present, together with the attachment of foreign bodies and detritus to it.

If a quantity of mud sufficient to form a thin layer over the bottom of the dish is present, a surface film of diatoms is formed over the mud surface immediately and binds the mud together. If the quantity of mud is small relative to the numbers of diatoms lying over it, it is characteristic of the film that within a few hours of its formation the whole structure has contracted a few centimetres away from the sides of the dish. The presence of a few *Oscillatoria* filaments appears to facilitate the formation of the film: the longer filaments help to form a supporting network. The spreading of the film from a central mass of mud is followed closely by the migration out over the film of many ciliates which are always found in association with it—particularly the strongly thigmotactic forms such as *Chlamydodon* or *Chilodon calkinsi*. Somewhat similar processes are reported by Picken (1937) for freshwater associations.

In the laboratory, if material developing a film is kept immersed in the original water sample, conditions soon become unsuitable for diatoms owing to the rapid decomposition brought about by the growth of bacteria. The film breaks up and disappears in about five days and the mud surface develops a crumby appearance.

Microscopic examination shows that breakdown of the film is accompanied by death of most of the ciliates usually associated with it. Doubtless bacterial attacks upon the mucilages and other substances composing the film are responsible for its breakdown, and the cessation of diatom activity results in a failure to replace it by any fresh secretion.

It has been observed that as the tide ebbs in the runnels, the diatoms have disappeared from the mud surface, but they rapidly reappear in small patches of colour which eventually coalesce as they are uncovered. Aleem (1950) describing the diatom populations at Whitstable, states that the diatoms burrow during inundation, and that they do not go below the surface until they are actually covered by the tidal water, reappearing again some time after the tide has receded. He considers that changes in light intensity are the stimulus to this behaviour. Such behaviour may reduce or prevent their dispersal by the tide. The phenomenon is problematical, however, as my observations suggest that in some of the habitats which are protected from the full mechanical action of the tide, such as pools with shelving sides and overhanging vegetation, the diatom films do not disappear at each tide. Here the diatom films are visible as soon as the water recedes. This is also noticed in habitats where the tide flows gently over the flat mud surface as a continuous sheet of rapidly advancing water. In the runnels, on the other hand, the restriction of the water to a narrow deep channel builds up a current, the force of which may cause considerable disturbance of the bed and banks, and consequent dispersal of the diatoms.

A series of day-to-day examinations was made during the spring tides of April 1951. In the runnels containing stations A and B (Fig. 1) a strong current is developed during both the ebb and flow of equinoctial spring tides, and the scouring action of the current breaks up any formed film completely; there is practically no reformation of the film during low tides. Over a period of five days these two stations contained a very sparse population of Protozoa with an almost complete absence of thigmotactic forms. During the same period stations C, D, E, F and I were covered by each tide and then exposed, but the diatom films in these habitats were not broken up and the protozoan communities remained relatively stable in composition both before and after high tide, even though at stations C and E there was an appreciable current especially during the ebb tide. During neap tides, and at other times of the year when springs are not so high or so violent, a well-defined film was observed in runnels A and B during low tide, and may be maintained even when the runnels are full at high tide. The stability of the film is also illustrated by the observation that in stations F and E, small areas of film removed on the first day of examination had not been replaced even after a period of five days. Evidently in the natural environment recolonization of bare areas takes some time. Ideally it may be supposed that for maximum efficiency a layer of diatoms exposed to the light would be one or two cells thick to obtain maximum radiation for photosynthesis, i.e. an arrangement similar to the top two chloroplast-containing layers of palissade cells in the normal mesophyte. Observations indicate that the diatoms tend to orientate themselves so as to utilize all available surface. At the

same time, they always remain in close proximity, glissading over one another and constantly changing position. The coherent properties of their mucilage sheaths doubtless help to account for their gregariousness, which probably partially explains the time taken to recolonize areas from which the film has been removed. Their mutual attraction overcomes their tendency to utilize all available surface, at least for a period. The recolonization of bare areas may also depend upon the deposition of suitable fine silt particles over the area by tidal action, together with conditioning of the surface by the secretions of the organisms themselves. The production of polysaccharides by bacteria may be a preliminary in the formation of the film, as bacteria are always abundant in the mud even before diatom associations become established.

Certain conclusions emerge from these observations. Firstly the diatoms are generally not dispersed by the tide but are retained in their habitats, either by submergence in the upper mud layers, or with the help of the film lying on the mud surface to which they are bound by their mucilaginous sheaths. Secondly the film appears to be essential for the development of ciliate communities. Many of the ciliates are bound to the film by their thigmotactic behaviour, which ensures that they are restricted to the regions in which food aggregations occur and also to some extent protects them against tidal disturbance. Furthermore the film binds together the upper layers of the silt, prevents dispersal of the silt particles and their associated nutrients by the tide, and reduces the degree of desiccation of the surface during periods of exposure. It appears to condition the mud surface in some way, making it suitable for other micro-organisms. This property can only be deduced from observations that communities take several days to develop in areas from which the film has been removed; their reformation does not automatically follow upon the deposition of typical organisms by the tide. In places where the film is lacking, even where abundant bacteria may provide a food source, only isolated ciliates are found and an organized society never appears.

(*d*) *Social structure*

The Ciliophora occur in communities together with the diatoms and bacteria. Provided the necessary diatom film exists as a physical basis, the factor determining the basic composition of a community is available food. In the marsh habitats there is never any division into the two types of ciliate community described for fresh-water ciliates by Noland (1925) and Picken (1937) —i.e. the predominantly 'algal' and predominantly 'bacterial' types of association. On the marshes the bacteria aggregate in the greatest concentrations in the same regions as the diatoms, and tidal action tends to disperse local aggregations of bacteria over the diatom film, the major part of which is not dispersed. The habitats also contain much detritus. Bacteria, diatoms and detritus are the major food sources upon which the ciliate communities are based and all three types of food are fairly evenly distributed throughout the habitats.

The diatom film, with its associated bacteria and detritus, is continuous over large areas, and the collection made from each station is only a small sample of the

total population, representing a cross-section in time and space. Such a sample, of approximately 4 sq. in., may contain many distinct aggregations of ciliates, which may perhaps be regarded as separate micro-communities of dynamic constitution. The social structure of these communities will fluctuate in time and space as the composition of the microflora changes, according to the specific food requirements of the ciliates concerned. Socially integrated communities are built upon local concentrations of different types of food; aggregations of a single species of diatom certainly occur and the rapid rate of multiplication of bacteria must result in similar aggregations of these also. The high viscosity of the film retards diffusion, and the accumulation of metabolites, etc., may set up concentration gradients within the microhabitats. These chemical gradients may be of great significance in the initiation of abundant growths of particular baterial or algal species, the localization of which will lead to the localization of ciliate species. The key to a better understanding of the development and maintenance of the communities lies in a more exact analysis of the chemical changes occurring.

Table 6. *Food of the commoner marsh ciliates*

Subsidiary food sources are indicated in parentheses

Group I.	Diatoms
	Chilodon calkinsi (bact.?)
	Chlamydodon mnemosyne
	C. triquetrus
	Condylostoma patens (det.)
	C. patulum (bact.?)
	Frontonia marina (bact.)
	Strombidium elegans (bact.)
	S. styliferum (bact.)
Group II.	Bacteria
	Cohnilembus pusillus
	Euplotes charon (det.)
	Mesodinium acarus (?)
	M. pulex (?)
	Micromitra retractilis
	Pleuronema crassum
	P. marinum
	Spirostomum loxodes (dia.)
	S. teres (dia.)
	Stylonychia pustulata (dia.)
	Vorticella microstoma (det.? dia.?)
Group III.	Bacteria and detritus
	Aspidisca crenata (dia.)
	Aspidisca sp.
	Blepharisma salinarum (dia.)
Group IV.	Diatoms and bacteria
	Chilodontopsis elongata
	Cryptopharynx setigerus
	Diophrys appendiculatus (det.)
	D. scutum (det.)
	Placus socialis
Group V.	Bacteria, diatoms and detritus
	Euplotes harpa
	Holosticha kessleri
	Opisthotricha parallelis
	Uronychia transfuga (protozoa)
Group VI.	Protozoa
	Lacrymaria coronata
	L. lagenula
	L. olor var. *marina*
	Lionotus fasciola
	L. folium
	Loxophyllum fasciolatum
	L. helus
	L. meleagris
	L. setigerum
	L. undulatum
	Trachelocerca fusca
	T. phoenicopterus
	T. subviridis
Group VII.	Histiophagous species
	Provodon discolor
	Placus socialis

The diversity of the food supply is reflected in the versatile feeding habits of the ciliates. These may be roughly classified according to the type of food which constitutes the bulk of their diet, but very few species feed solely on one food source. The majority of the marsh ciliates take a mixed diet, although one particular type of food organism may dominate the diet of many species. The

commoner ciliates may be classified into six major groups according to their feeding habits. Groups I and II include a few species which feed exclusively on one particular source of plant food (either diatoms or bacteria respectively), as well as a larger group of species which, although feeding largely on one or other of these food sources, also take small quantities of other types of food and may change their diet if their normal major food source fails. These groups usually occur in large numbers in a particular locality, associated with a high concentration of a suitable food, or occur as rare, dispersed individuals. Exclusive diatom feeders (e.g. *Chlamydodon* spp.) exhibit this type of behaviour; single species are often found in very large numbers forming the basic members of a typical community. Numbers of exclusively bacterial feeding species are smaller. Forms with more versatile feeding habits (groups III, IV and V) are ubiquitous. They are frequently found in collections from all stations, but rarely in large numbers in a single locality. Predators (group VI) are widely distributed; the variety of predatory species in any one collection is often large compared with the number of non-predatory species, but the number of individuals of a predator is small, except occasionally in very dense populations of a suitable prey. Finally, two histiophagous forms have been observed (group VII; *Prorodon discolor*, *Placus socialis*) which feed on the cytoplasm of cytolysed ciliates in cultures. They are rare in the field where the function of scavenging is filled by the large bacterial population.

Quantitatively, the different groups appear to conform to the pyramidal structure characteristic of communities in the field. A typical community contains a large number of diatom feeders, often monospecific, and also some exclusive bacterial feeders. These strict herbivores form the largest percentage of a population. Then there is usually a smaller proportion of ciliates with more variable feeding habits (groups III, IV and V). In cultures these forms usually appear after groups I and II have died out, suggesting that they can utilize those bacteria and diatoms and also the detritus which are of no value to groups I and II. Predators will also multiply in a flourishing community. No predator has ever been observed to attack the larger diatom feeders (*Chlamydodon*, *Frontonia*); possibly size is an obstacle.

The composition of two typical communities is illustrated in Table 7.

Field collections kept in the laboratory become unsuitable for the continued growth of diatoms; the film breaks up and the diatoms either die or form gemmules within about five days, but the bacteria multiply enormously. Study of the sequence of such cultures can give information about the bacterial feeders and the possible community which might develop in the absence of living diatoms. The initial population of diatom feeders disappears within two or three days; an exception is *Frontonia marina* which, although normally feeding on diatoms, has been maintained for up to a fortnight in cultures which contained few living diatoms but large numbers of bacteria. The second and third days are marked by the enormous increase of bacterial feeders (e.g. *Pleuronema marinum*, *Euplotes charon*) or species which feed on small diatoms and bacteria, notably *Placus socialis* which feeds upon dead ciliates when these are available. By about the

fifth day these species have been replaced by a wide variety of forms eating bacteria and detritus, e.g. *Holosticha kessleri*, *Uronychia transfuga*, *Diophrys* spp., *Euplotes harpa*, *Blepharisma salinarum*, *Opistholricha parallelis*, *Aspidisca crenata*, etc. The populations of these forms may be increased by the addition of nutrients such as plant infusions, wheat grains, etc. In the field, these species normally occur as scattered individuals, possibly because dense aggregations of suitable foods rarely occur under natural conditions. The occurrence of predators depends upon the type and availability of prey, and thus ultimately upon the basic available flora.

Table 7. *The composition of two typical associations*

Group	Species	Abundance (Table 3)	Food
	Station B	3 May 1950	
I.	*Chilodon calkinsi*	s	smallest diatoms
	Chlamydodon triquetrus	a	large diatoms
	Strombidium elegans	+	medium and small diatoms (bacteria)
II.	*Pleuronema marinum*	+	bacteria
	Euplotes charon	f	bacteria (detritus)
	Mesodinium acarus	+	bacteria (detritus?)
III.	*Aspidisca crenata*	+	bacteria, detritus
V.	*Holosticha kessleri*	+	bacteria, small diatoms, detritus
VI.	*Lacrymaria olor*	+	protozoa
	Loxophyllum helus	+	protozoa
	? *Heminotus caudatus*	+	? protozoa
	Station F	20 Dec. 1950	
I.	*Chlamydodon mnemosyne*	+	medium and large diatoms
	Frontonia marina	+	large diatoms
	Strombidium elegans	f	small and medium diatoms
II.	*Euplotes charon*	+	bacteria (detritus)
IV.	*Diophrys appendiculatus*	+	small diatoms, bacteria (detritus)
V.	*Holosticha kessleri*	f	diatoms, bacteria, detritus
	Uronychia transfuga	+	diatoms, bacteria, detritus
VI.	*Lionotus folium*	+	protozoa
	Loxophyllum helus	+	protozoa
	L. setigerum	+	protozoa

FOOD SELECTION IN THE CILIATA

The importance of total available food as a factor controlling the development of protozoan populations is generally recognized, but little consideration has been given to more specific feeding relationships. The bacterial feeders recorded from the marsh habitats are mostly discontinuous feeders, periods of swimming alternating with periods of locomotory quiescence, during which the feeding mechanism is active. *Pleuronema marinum* is characteristic of this group. Short infrequent periods of locomotion may enable *P. marinum* to congregate in areas containing a suitable bacterial flora. Aggregations of this kind are often observed. When the food supply fails, the locomotory periods may become longer or more frequent, enabling the ciliate to explore a wider territory. Behaviour of this type may account for the localization of bacterial feeders. Luck, Sheets & Thomas (1931) and Leslie (1940) have demonstrated that different types of bacteria may differ considerably in their suitability as food for ciliates.

In forms other than bacterial feeders, size of food organisms is probably a most important consideration. The numerous diatom feeders observed all appear to have their optimal size of diatom. They may be listed according to the increasing size of their normal food thus: *Chilodon calkinsi, Cryptopharynx setigerus, Strombidium elegans, Chilodontopsis elongatum, Condylostoma patens, Chlamydodon mnemosyne, C. triquetrus, Frontonia marina.*

There is a general relationship between average size of the most abundant diatoms and the dominant diatom-feeding species in a particular microhabitat. It may be tentatively suggested that this relationship explains the typical distribution of the marsh diatom feeders. Commonly, two or three species of diatom feeder occur together in a habitat and they are usually feeding upon different-sized diatoms, e.g. *Chlamydodon triquetrus* and *Chilodon calkinsi* may occur in the same collection, but it is only rarely that one finds abundant populations of two species feeding on the same size groups of diatom, e.g. *Chlamydodon triquetrus* and *Frontonia marina.*

The occurrence of *Nassula citrea* appears to be strictly determined by the presence of a certain type of food. It occurs infrequently and has only been found in association with abundant filaments of *Oscillatoria.* When first collected, *Nassula citrea* was always filled with bright green contents, making identification difficult. The ciliates were maintained in the laboratory for a few days, and during the first day or two they fed on the *Oscillatoria* by taking in the filaments through the armed cytopharynx; the filaments are gradually coiled in the cytoplasm, sometimes deforming the animal temporarily. Once this food supply was exhausted, *Nassula citrea* did not feed at all, although diatoms and other algae were abundant and were utilized for several days by other ciliates in the culture. *N. citrea* swam about until the contents of the food vacuoles were digested and the cytoplasm became transparent and slightly orange-coloured. Many of the starved individuals encysted. Experiments demonstrated that *N. citrea* is positively phototactic and as the *Oscillatoria* shows a similar response to light, the behaviour of the ciliates may enable them to collect in areas where the food organism is abundant. *Strombidium elegans,* which feeds upon small diatoms, is also positively phototactic.

Lund (1933) considers that size and shape of food may influence food selection amongst holozoic ciliates. Observations made during the present study support this view. In particular, the feeding habits of *Diophrys appendiculatus* have been observed while attempting to find a suitable culture medium for this hypotrich. It multiplies in old enrichment cultures, in which it feeds upon the rich, mixed bacterial flora and upon detritus. It feeds and multiplies upon baker's yeast, *Saccharomyces cervisiae,* but not so successfully on the smaller-celled wild strain, *S. exiguus.* Populations have been maintained and have increased while feeding on a small round *Chlorococcus*-like alga and on wheat starch grains. In the latter case, large quantities of bacteria were undoubtedly ingested together with the visibly ingested starch grains. If offered a choice, *Diophrys appendiculatus* feeds on small diatoms but not on large ones, although it will utilize slightly larger diatoms than usual if no small ones are available. The foods upon which the populations

increased, at least initially, were all of similar size and shape, i.e. yeast cells, small round algae, starch grains and small diatoms. There is therefore some evidence that size and shape of food are important in the food selection of this ciliate.

The morphology of the feeding organelles is correlated with the feeding habits of many ciliates by Lund (1941). Observations of this type might help to explain the restriction of some species to narrowly defined habitats containing a particular type of food. The behaviour of ciliates in laboratory cultures may be illuminating. Thus, *Frontonia marina*, which normally utilizes large diatoms, will flourish in yeast cultures and also in cultures supporting a mixed bacterial population. *Frontonia* has a complicated system of cytostomal fibres and well-developed peristomal fibres (Bullington 1939). According to Lund (1941) fibre mechanisms of this type enable ciliates to ingest various types of food; particle size is unimportant. On the other hand both species of *Chlamydodon*, normally feeding on large diatoms, appear to be incapable of modifying their feeding habits in the absence of their usual food. *Chlamydodon* normally ingests algae by means of a pharyngeal basket and only possesses a small membrane covering the pharyngeal opening, pierced by a slit for the admission of food (MacDougall 1928); it therefore has no mechanism for concentrating small particles such as bacteria in the region of the pharyngeal opening. The structure of the feeding organelles may possibly explain the ability of many forms such as *Holosticha kessleri*, *Uronychia transfuga*, *Opisthotricha parallelis*, etc. to ingest a wide variety of foods both in the field and in the laboratory. This relationship has not been investigated for these species.

The predatory ciliates attack living prey; selection is therefore a possibility and there is some evidence that it occurs. It is well known that *Didinium nasutum* exclusively attacks *Paramecium*. Lilly (1942) states that the facultative predators *Stylonychia pustulata* and *Pleurotricha lanceolata* will feed upon a variety of small ciliates, including *Tetrahymena*, but refuse dead *Tetrahymena*, indicating some powers of discrimination.

Fauré-Fremiet (1951) describes how predators often occur as very small isolated individuals, which increase in size and multiply in the presence of suitable prey. *Lacrymaria olor* var. *marina* is a predator found in the marsh habitats. It is ubiquitous, occurring in all the stations from time to time as well as in the surface sand of the littoral zone away from any diatom growths. In field collections it occurs as isolated specimens, often rather small and lacking food vacuoles. It has been cultured in the laboratory in wheat grain cultures inoculated with field material, which favour rapid multiplication of *Cohnilembus pusillus*. If a few *Lacrymaria* are inoculated into a rich culture of *Cohnilembus*, they attack and devour enormous numbers. The predators increase in size and divide, and within a few days there is a flourishing population of *Lacrymaria* and a visible reduction in numbers of *Cohnilembus*. Finally, when the food supply is exhausted, many of the *Lacrymaria* encyst. In old cultures with few *Cohnilembus* and many small specimens of *Diophrys* and *Uronychia*, *Lacrymaria olor* attacks the hypotrichs, but not always with success, as the hypotrichs appear to be more resistant to the paralysing effects of the predator than is *Cohnilembus*. The prey of *Lacrymaria olor* in the field is rather

problematical. *Cohnilembus* is very rarely found, and *Lacrymaria* has not been observed to attack other ciliates in field collections. The fact that it will attack hypotrichs, suggests that it can utilize a variety of forms. *L. coronata* is observed to feed and multiply on the cysts of *Nassula citrea* and a species of *Glenodinium*. In cultures, *Loxophyllum* preys upon *Diophrys appendiculatus*; the prey can be seen struggling in the food vacuole for some time after ingestion. *Loxophyllum setigerum* also ingests the cysts of *Diophrys appendiculatus*. Ingestion of protozoan cysts by ciliate predators appears to be quite common.

Uronychia transfuga presents an interesting example of a facultative predator. Although normally an omnivorous feeder utilizing algae, bacteria or detritus, in media in which there was very little food, it was observed to attack and ingest small specimens of *Diophrys appendiculatus* as large as itself. The struggling *Diophrys* projected from the peristome for several minutes after the attack and when finally engulfed filled the body of the *Uronychia* almost completely.

DISCUSSION

A major problem in attempting to analyse communities of micro-organisms is the definition of environmental conditions. The crude methods employed to determine temperature, salinity, hydrogen-ion concentration, etc. give little indication of the actual conditions in which the micro-organisms live. Adequate methods of microanalysis of such conditions are perhaps unattainable.

Earlier workers considered that protozoan populations must be influenced by the seasonal and environmental changes governing the ecology of larger animals. Noland (1925) showed that food supply is of major importance in determining the occurrence of ciliates in a particular habitat. He observed that although variations in individual environmental factors may bear no close relationship to population trends, the whole physical and chemical complex is vitally concerned in providing a suitable milieu for the development of those food organisms on which the population is based.

Many ciliates are known to be tolerant of a wide range of environmental change; given the necessary conditions for the production of an adequate food supply, one would expect to search for finer ecological boundaries than the limitations imposed by seasonal and tidal changes. Picken (1937) considers that:

'1. Protozoa occur in societies having a considerable degree of social organization.

2. The origin, persistence and decay of such communities is determined by relatively simple mechanical forces.'

He emphasizes that analogous functions in a community may be fulfilled by systematically unrelated types. Fauré-Fremiet (1950*a*) indicates the succession of ciliate forms occurring in a typical freshwater community and reaches conclusions in fundamental agreement with those of Picken.

My observations substantially support the views of Picken and Fauré-Fremiet. The Ciliophora of the marshes exist in societies having a clearly defined structure of

a basic population of diatom-eating and bacterial-eating herbivores, a smaller number of animals of more diverse feeding habits, and a few predators. The structure of these communities always follows the same plan, but the individual niches in the social structure may be filled by a variety of systematically unrelated species, one of which is dominant at any particular time. Once a species has exhausted its specific food in a region, its representatives disperse to discover new sources and it may be replaced by a species filling a slightly different niche. Correlated with the high degree of organic pollution, the microflora is more varied and considerably more abundant than in most freshwater habitats. The uniformly superfluous food supply maintains the ciliate communities continuously, in contrast to the associations described by Fauré-Fremiet and Picken, where communities may be rapidly built up in a particular locality and then disintegrate and disperse as the food supply fails. The specific composition of the marsh communities shows continuous change, however, as the composition of the microflora changes. The diet of the ciliates is controlled by size and shape of food, and probably also by biochemical differences in the constitution of the food organisms available. Consequently as a particular food species is depleted, a ciliate using that food source will decline in numbers, to be replaced by another species utilizing a different food source now abundant.

In the marsh communities, the films produced chiefly by diatom activity over the mud surfaces create the structural basis which Picken (1937) considers is provided by filamentous algae in freshwater communities. The diatom associations differ from Picken's associations in that the diatoms not only provide a structural basis for the community but they are a source of food as well. According to Picken the thallophytes forming the mechanical basis of the freshwater communities are not consumed by the ciliates until the algal filaments die and the community breaks up. It is interesting to note that Picken rarely found ciliates associated with large aggregations of diatoms.

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SUMMARY

1. In a survey of the Ciliophora occurring in brackish water at Parkgate, Cheshire, sixty-one species are recorded. Distribution of the commonest species cannot be directly related to seasonal or tidal change or to gross fluctuations in temperature, salinity or hydrogen-ion concentration.

2. The ciliates recorded may be classified according to whether they occur in the interstitial spaces of the mud or associated with the diatom films. Many species in the latter group may be found occasionally in the inter-granular spaces, but achieve their greatest numbers in association with the films. A few species occur exclusively in the interstitial spaces, and a few species are always found attached to the diatom films. The latter are all diatom feeders and may attain large numbers of a single species at any one time.

3. The ciliates associated with the diatom films occur in communities having a distinct social structure, which is described. The occurrence of these communities depends upon: *a*, the presence of an abundant microflora, consisting of bacteria and diatoms, as a source of food; *b*) the presence of a film of organic matter, produced mainly by the secretory activities of the microflora.

4. It is suggested that the composition of the ciliate fauna may be influenced by the biochemical suitability of the available microflora as food, together with its suitability of size and shape in relation to the feeding mechanisms of the ciliates concerned.

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REVIEWS

ANIMAL NUMBERS

Lack, David (1954). *The Natural Regulation of Animal Numbers.* Pp. viii + 343; 1 plate and 52 text-figures. Oxford: Clarendon Press. Price 35*s*.

This book is a sound and valuable contribution to one of the most important aspects of ecology. It is a book in the best traditions of English scientific natural history: those traditions of careful observation of Nature and profound deduction of which *The Origin of Species* is the classic. *The Natural Regulation of Animal Numbers* is well written, the arguments are gently and lucidly explained and developed and no biologist should find any part difficult or uninteresting. The production is of high quality with clear text-figures and good printing, though the paper is rather heavy. Each chapter ends with a brief and useful summary, and the list of several hundred references and the two indices are admirable.

It must be said at the outset that the author is an ornithologist and about three-quarters of the material discussed in the book is about birds. Further, the book has been deliberately limited to evidence from natural wild populations, only slight reference is made to laboratory populations or mathematical models, and evidence from man-managed or exploited populations is used sparingly. This does not mean that non-avian animals are neglected, and the author has throughout been very conscious of the basic implications to all animals of the ideas he has developed largely from the studies of birds. Non-ornithologists, particularly perhaps entomologists and laboratory ecologists, may feel that evidence from their animals has not been adequately utilized and developed, but it is doubtful if it is now within the powers of one man to integrate successfully the data available from all kinds of animal populations. In fact we should be very grateful to have available such an excellent summary of the ornithological literature alone.

After reading this book one is conscious of the wealth of data collected by ecologists that is irrelevant to the main problems with which they should be concerned, and by contrast, how much light can be shed on these problems when the collection of even a small set of data can be carefully and specifically designed to answer a real and relevant question. Dr Lack and some of his fellow-ornithologists can set an example to many other ecologists in this respect. The author cannot therefore be blamed if the evidence available is often not adequate for the needs of the discussion, which occasionally becomes rather loose as a result. Sometimes the conclusions seem weightier than the data from which they were derived, but at other times I felt that a more forceful and dogmatic argument was justified, if only for the stimulus it would have provided. On the whole, however, a happy balance has been struck between information and theory. Not all ecologists will support all the conclusions, but I suspect that most will agree that they are the result of a careful weighing of evidence and clear and logical thought. As a result, most of the conclusions seem very reasonable and will probably provide good working hypotheses and the necessary stimulus for the collection of further relevant data.

The first part of the book deals with reproduction and the factors influencing fecundity. It is concluded that in birds and many other animals there is little evidence of fecundity being related to density. The chapters on clutch size in birds are particularly interesting, as it is shown that a strong density-dependent mortality operates among nestlings and the number of eggs laid by a bird is usually that which will, on average, give rise to the

largest number of fledglings. A clear and valuable emphasis is laid here on the distinction between ultimate and proximate factors.

The second part of the book reviews mortality and its causes. Survival curves and mortality rates for adult wild birds and some other animals are given; a fair amount of information is now available, but it is clear that very little is known about the mortality of juvenile animals. Food, predation and then parasites and diseases are discussed as factors causing mortality. It is concluded that, in general, food shortage is the principal mortality factor that is density-dependent but that predation, parasites and disease may sometimes be important and are often complicating factors. Thirdly there is a series of chapters dealing with other features of populations, such as climate, cycles, territory, irruptions and migrations. These contain a great deal of interesting information, mainly on birds, and the chapter on cycles seems a particularly good summary while at the same time it reveals that very few careful and detailed observations have in fact been made on cyclic populations. A brief concluding chapter summarizes the main thesis and mentions some practical aspects of animal populations.

It is tempting, in finally assessing this book, to compare it to Andrewartha and Birch's book *The Distribution and Abundance of Animals* (1954). Both books, broadly speaking, deal with the same subject, and a little of the evidence used by them is the same, but there the resemblance seems to end. Even a superficial glance is enough to show that 'density-dependent mortality' is an anathema to Andrewartha and Birch, while it is the backbone of Lack's book. Perhaps it is a commentary on the present position of animal population ecology that two such books, both sound and both stimulating, yet with apparently little else in common, should be published in the same year. I suspect, however, that much of the apparent incompatability of the two schools of thought is really a matter of terminology and emotion, and that the ideas are complementary rather than antagonistic. Probably both books should be read by all ecologists; Lack's certainly should.

E. D. LE CREN

ECOLOGY FOR STUDENTS

G. L. Clarke (1954). *Elements of Ecology*. Pp. xiv + 534; about 200 text-figures. New York: Wiley; London: Chapman & Hall. Price 60*s*.

This book is written primarily for students and is based on a course of lectures given by the author. He takes one by one the factors that influence organisms, such as light, temperature, other creatures, and so on, and devotes a chapter to each, concluding with chapters on the community, succession and fluctuation, and dynamics of the ecosystem. The impression created is that in American universities, as was certainly the case in British ones when the reviewer was a student, zoology is mainly the study of dead animals in dishes and little is taught about what the living do. The author, aware of this gap to fill, has felt obliged to pack a great deal of information of a distinctly varied nature into his pages. Moreover each physical and chemical factor is treated comprehensively, and the result is a book full of facts which are carefully marshalled and clearly described, but which are so numerous that no particular line of thought can be followed very deeply.

So many books have appeared recently on ecology that comparative remarks may be welcome in a review even though the reviewer makes no claim to have explored the whole field. Woodbury (1954) *Principles of General Ecology* (New York and Toronto: Blakiston) provides an even broader base for his readers, and there are for example five pages devoted to the universe in the chapter headed 'Organisms and Environment'. On the other hand Odum (1953) *Fundamentals of Ecology* (Philadelphia and London: Saunders) with important chapters on limiting factors, energy in ecological systems, and interrelationships be-

tween organisms of the same and of different species, offers a more meagre diet of fact but a clearer conception of the problems in ecology. Those who deplore specialization as excessive concentration on a limited field will prefer the first two books; those who rate ideas more highly than facts the last. These three books are primarily for students and teachers. Practising ecologists, whose need is critical discussion of current controversies, will be saving up for a copy of Andrewartha & Birch (1954) *The Distribution and Abundance of Animals* (Chicago: University of Chicago Press; London: Cambridge University Press).

T. T. MACAN

DIAPAUSE

A. D. Lees (1955). *The Physiology of Diapause in Arthropods.* Pp. x + 151 25 text-figures. London: Cambridge University Press (Cambridge Monographs in Experimental Biology, No. 4). Price 12*s.* 6*d.*

The central ecological problem in what might be called the mystery of diapause is set out in the words of Kirby and Spence (1815) on the fly-leaf of Dr Lees's book:

'To refer the hybernation of insects to the mere direct influence of cold, is to suppose one of the most important acts of their existence given up to the blind guidance of feelings which in the variable climates of Europe would be leading them into perpetual and fatal errors . . . It is not, we may rest assured, to such a deceptious guide that the Creator has entrusted the safety of so important a part of his creatures.'

Their use of the word 'hybernation' is of some importance to us. It emphasizes the fact that the phenomena of diapause are widespread in animals and plants and Dr Lees does well to remind his readers that in origin 'Diapause' simply means 'rest' or 'interruption of work'. It is a pity that since its introduction by Wheeler in 1893 the word has tended to become an exclusively entomological term, creating a gulf between the problems of insect hibernation and those met with in other animals. But the fact remains that it is in the Arthropoda and particularly the Insecta, where normal growth is essentially discontinuous and where the ecological implications of the phenomena are widespread, that its study has received the greatest attention.

Diapause may occur in any of the major stages of an insect life history, in the egg, larva pupa or imago, and it is generally accepted that it usually occurs in that stage of the life-cycle best adapted to survive environmental conditions unfavourable for feeding and reproduction. Surprisingly enough, it need not necessarily occur in the same stage even in very closely related species. Although Dr Lees's main concern is with the physiological problems centred on the relations of endocrine secretions and changes in the metabolic processes of growth, he gives considerable attention to the ecological aspects of diapause. Thus, four of the nine chapters 'The environment and the onset of diapause', 'The environment and the termination of diapause', 'The rôle of water in the arrest of growth' and 'Diapause and phenology' are all concerned with environmental influences.

His full treatment of photoperiodism should interest ecologists. As he points out, of all the environmental factors that might indicate seasonal change ' . . . the length of day possesses all the necessary attributes. It is invariable, and the response can be so adapted that the insect can enter the resistant diapause stage before the advent of unfavourable seasonal conditions'. It seems in general that the photoperiodic reaction in arthropods is independent of intensity and total light energy, provided that a certain threshold value is reached. That the threshold appears to be just above the intensity of direct moonlight is obviously of some importance.

Modern research indicates the importance of endocrine secretions in the regulation of

diapause. The problem now facing the physiologists is to determine the precise role which the endocrine system plays in the series of events either leading up to its occurrence or bringing about its cessation. Dr Lees favours the view that the environmental factors acting on an insect influence the endocrine glands by way of the nervous system and that '. . . the central nervous system is the vehicle which carries and eventually transmits the "directions" of the environment'. As he admits, examples of maternally induced diapause, that is where the effects of the environment acting on the mother do not operate until some later larval stage, cannot be explained by his hypothesis. The reviewer, as one of the people who has described the occurrence of maternally induced diapause, can only point out that it is probably more widespread than the literature indicates. While it is satisfying to have a comprehensive theory, it is important, particularly in our present state of knowledge, to bear in mind that the actual mode of transmission of the diapause effect may differ between groups of organisms, and Dr Lees summarizes other views which have been advanced to explain it. This is an excellent monograph, well written and produced, which should serve to stimulate attention on the weak points in our present knowledge of arthropod diapause. Dr Lees is to be congratulated on bringing order into the extensive and widely scattered literature on this subject.

J. B. CRAGG

CALANUS

S. M. Marshall and A. P. Orr (1955). *The Biology of a Marine Copepod:* Calanus finmarchicus *Gunnerus*. Pp. vii + 188; 1 plate; 63 text-figures. Edinburgh: Oliver & Boyd. Price 21*s*.

Despite the overwhelming importance of the zooplankton in the economy of the sea there is no text which deals fully with the biology of any one species. The present volume by Marshall and Orr is therefore most welcome, and it is fitting that it deals with *Calanus*, perhaps the most widespread and best known member of the zooplankton and the subject of so much original work by the authors themselves. The early chapters deal with anatomy and distribution. There is a useful short section which touches on the different species of *Calanus* and on the old problem of the separation of *C. finmarchicus* and *C. helgolandicus*. It is pleasing to have well-illustrated accounts of both internal and external anatomy; the lack of studies on the internal anatomy generally of copepods is noteworthy. The painstaking analysis of the variation in setation of appendages throughout the different developmental stages (pp. 56-63) is a most useful contribution, and one which is very desirable for other planktonic copepods.

The general view of the book, however, is experimental. Under reproduction the duration and extent of egg-laying is discussed, and the authors show that there is a marked and rapid effect of feeding on egg production. Not only is the quantity of food important, but various phytoplankton foods are not equally effective in stimulating egg production. It will be interesting to see whether further work will show differences between various diatoms, and also whether cell-free filtrates from phytoplankton cultures can affect either egg production or feeding rates. The discrepancies which appear in the feeding rates of *Calanus* (pp. 106-10) might indeed partly arise from the age and condition of phytoplankton food cultures as well as from the different volumes of medium used. General conclusions on the time of egg-laying are not very clear. Marshall and Orr suggest that 'stimulus to egg-laying caused by capture and examination predominates in Tromsø waters', but apparently not elsewhere. Before accepting this suggestion, a critical appraisal of the changes in temperature and other environmental factors during capture and examination of the copepods from the different localities would appear necessary. Precise studies on the reproductive behaviour of male *Calanus*

are still awaited, and in view of the difficulties in keeping males, perhaps other copepods might be profitably investigated. The duration of the viability of the sperm is an interesting point. From field results in polar waters (p. 70) it appears that sperm must live for at least five to six months in the spermathecae.

The question of the life-cycle is very well reviewed and the variations in the North Atlantic area are adequately dealt with. It is curious that only two generations of *Calanus* per year are reported for the warmer waters south of Cape Cod. On the problem of size variation, the absence of any experimental data makes it difficult, as the authors admit, to assess the importance of such factors as temperature, generation and feeding, and there is the old difficulty of the wide size range. The changes in length and in dry weight, however, bear out the seasonal cycle suggested, though there appears to be a diminution in length of Stage V copepodites from September to January which is unexplained. It is also surprising that the fat content of females despite egg production changes less than that of males of Stage V.

The need for further detailed field and laboratory studies on *Calanus* is apparent especially with regard to depth distribution of the copepods. On seasonal migration, as the authors state (p. 124), 'there is no simple explanation of these movements to and from the surface'. One wonders how far the differences between the behaviour of *Calanus* from various regions are maintained over several years, and also how fully environmental conditions have been investigated. The great variability in the diurnal vertical migration with season, developmental stage, region and generation is rightly emphasized. Too little attention has been paid to these factors in laboratory experiment, and equally important here the 'physiological state' of the copepod, especially the effects of handling, must be taken into account.

The final chapter sheds a great deal of light on the whole subject of plankton ecology. One could have wished this to have been somewhat expanded. The authors express surprise that *Calanus*, although it can be acclimatized to lower salinities, has not colonized the Baltic. Surely, however, the acclimatization refers to adults or to older copepodites, and the young nauplii may be more sensitive to change. The problem of the survival of the over-wintering stock of Stage V, in view of winter food scarcity, remains one of the most difficult. The possibilities that *Calanus* may become partly carnivorous, and that over-wintering copepodites feed less actively and live at a reduced metabolic level, are well worth reinvestigation.

The present volume represents an excellent summary of the existing knowledge on *Calanus* and the authors demonstrate the need for future research. The book is well produced and clearly written and it is refreshingly free from printing errors. It will be welcomed by all who are interested in zooplankton and indeed by all marine ecologists.

J. E. G. RAYMONT

BEHAVIOUR IN CAPTIVITY

H. Hediger (1955). *Studies of the Psychology and Behaviour of Captive Animals in Zoos and Circuses* (Translated by Geoffrey Sircom). Pp. vii + 166; 16 plates. London: Butterworth. Price 30*s*.

The title given to this book, one presumes by the British publisher, does it a disservice since it leads the reader to expect something more ambitious and more authoritative than it in fact sets out to be. The original German title 'Skizzen zu einer Tierpsychologie im Zoo und im Zirkus' is both more honest and more accurate. The author himself claims nothing more for it than a record of 'casual finds from the zoo, fully aware that they are merely fragments—scattered and unpretentious tesserae'. In keeping with this the book

is in the main anecdotal and may be considered supplementary to, though much slighter in substance than, the author's previous work, *Wild Animals in Captivity*.

There can be no doubt about the degree of intelligence and insight which Dr. Hediger brings into his studies of the behaviour of animals. British students of behaviour, however, are likely to be cautious in accepting the interpretation offered of many of the actions described, a caution which is rooted in differences of long standing in the intellectual climate of British and Continental schools of psychology. The study of behaviour is the study of animals' movements, and strictly speaking that is what this book is about, while animal psychology, if it means anything, must be regarded as the more sophisticated attempt to interpret what is going on within them. At the present time one doubts whether this approach adopted in this book is likely to lead to any notable advance in our knowledge of the organization of behaviour in higher animals. With these reservations the book is wholly delightful to read and is full of fascinating observations, of which a high proportion are the author's own. The translation is excellent.

D. M. STEVEN

BIRD NAVIGATION

G. V. T. Matthews (1955). *Bird Navigation.* Pp. vii + 141; 33 text-figures. Cambridge: Cambridge University Press. Price 12*s.* 6*d.*

As one of the *Cambridge Monographs in Experimental Biology* this book might be thought to have little to offer to the ecologist. In fact, however, that is very far from the case, since it provides a most striking demonstration of the kind of way in which the experimental method can be brought to bear on what has been widely regarded as essentially a 'field' problem, as well as of its effectiveness in producing results.

The first four chapters consist of a critical survey of the evidence both experimental and observational. They lead Dr Matthews to the conclusion that there is clear evidence for two kinds of navigational ability, a simple type, which may be either innate or learnt, in which the bird flies only in one particular direction, and a type of complete navigation which enables the bird to orientate and to fly towards a known goal, no matter in which direction it has been displaced. In this latter type 'the orientation process is innate, but learning is involved in its successful operation and its relation to a particular "home"'. Various theories proposed to provide mechanisms for both these are then considered against the background of the experimental evidence, and most of them are rejected as improbable or untenable. Dr Matthews then puts forward his own theory according to which the bird observes the apparent arc in the sky traversed by the sun during a comparatively short period of time, extrapolates this to its point of maximum altitude, thereby obtaining a south point from which to orientate its direction of flight. The implications of this mechanism are discussed in detail with the results of the ingenious experiments Dr Matthews has carried out in order to test his hypothesis.

Although not all the arguments used are equally rigorous there is a substantial basis for the theory, and the book is for the most part closely argued; the style is clear and terse.

H. C. GILSON

BOOKS RECEIVED

Elements of Zoology. By TRACY I. STORER and ROBERT L. USINGER. New York, Toronto and London: McGraw Hill. 1955. Price 41*s*. 6*d*.

The Numbers of Man and Animals. Edited by J. B. CRAGG and N. W. PIRIE. Edinburgh and London: Oliver & Boyd (for the Institute of Biology). 1955. Price 15*s*.

South African Animal Life. Edited by BERTIL HANSTRÖM, PER BRINCK and GUSTAF RUDEBECK. Vol. I. Stockholm: Almquist & Wiksell. 1955. Price *Sw. kr*. 68.

Djuren i Färg. By K. CURRY-LINDAHL. Stockholm: Almquist & Wiksell. 1955. Price *Sw. kr*. 8.75.

Red Foxes and a Declining Prey Population. By THOMAS G. SCOTT and WILLARD D. KLIMSTRA. Carbondale, Ill.: Southern Illinois University. 1955. Price $2.00.

Toxic Chemicals in Agriculture: Risks to Wild Life. Report of the Working Party. London: H.M.S.O. (for the Ministry of Agriculture, Fisheries and Food). 1955. Price 1*s*. 6*d*.

Soil Zoology. Edited by D. K. MCE. KEVAN. (Proceedings of the University of Nottingham Second Easter School in Agricultural Science, 1955.) London: Butterworth. 1955. Price 55*s*.

Kieler Meeresforschungen. Bd. XI, Heft 2. Edited by G. WUST and A. REMANE. Kiel: Institut für Meereskunde an der Universität Kiel. 1955. No price given.

The Nuffield Foundation: Tenth Report for 1954-55. Oxford. 1955.

Poultry Breeding. By G. E. MANN. (Ministry of Agriculture and Fisheries Bulletin No. 146). London: H.M.S.O. 1955. Price 4*s*. 6*d*.

ABSTRACTS

Abstracts are now appearing from the following journals and publications:

Agriculture
Ann. Appl. Biol.
Ann. Mag. Nat. Hist.
Antiquity
Biol. Rev.
Biometrika
Bird Study
Brit. Birds
Brit. J. Anim. Behav.
Bull. Ent. Res.
Bull. Mammal Soc. Brit. Is.
Coll. Repr. Scot. Mar. Biol. Ass.
Countryside
Discovery
Endeavour
Entomologist
Ent. Mon. Mag.
Ent. Rec.
Fish. Invest. Lond.
Ibis
J. Conchol.
J. Gen. Microbiol.
J. Hyg., Camb.
J. Mar. Biol. Ass. U.K.
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Linn. Soc. Lond. Proc. & Trans.
Lond. Naturalist
Naturalist
Nature Lond.
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Proc. Zool. Soc. Lond.
Quart. J. Micr. Sci.
Rep. Dove Mar. Lab.
Rep. East Malling Res. Stn.
Rep. Mar. Biol. Stn. Pt. Erin
R. Ent. Soc. Proc. & Trans.
Roy. Soc. Proc. & Trans.
Roy. Soc. Edin. Proc. & Trans.
Salm. Trout Mag.
Sci. News
Scot. Agric.
Scot. Home Dept. Sci. Invest.
Scot. Nat.
Welsh J. Agric.

and the journals and proceedings of local natural history societies.

There remain a few journals, notably those covering forestry, which it is still impossible to abstract and offers of assistance are still sought for these.

The abstracts are edited by Professor L. A. Harvey with the assistance in selection and abstracting of J. D. Brayshaw, G. I. Crawford, T. A. W. Davis, A. E. Ellis, P. D. Gabbutt, Miss U. Grigg, N. A. Holme, S. J. Holt, D. Leatherdale, A. Macfadyen, C. Matheson, E. J. Moynahan, Miss E. Nelmes, W. R. Pickering, J. L. Cloudsley-Thompson, G. G. Vickers, Mrs M. Vincent, M. Williamson and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Professor L. A. Harvey, University College, Exeter.**

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Back numbers of the 'Notices of publications . . .' from Vol. 3 (1934) to Vol. 20 (1951) may also be had at 2*s.* for each annual set of two parts.

CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *Bird Notes* and *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above two journals and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Allen, J. A. (**1954**). On the structure and adaptations of *Pandora inaequivalvis* and *P. pinna*. *Quart. J. Micr. Sci.* **95**, 473-482.

Includes an account of the ciliary mechanisms of the mantle and of the gills; the habit; and the functioning of the stomach.

Chubb, J. C. (**1954**). Observations on oiled birds, 1951-53. *Northw. Nat.* (N.S.) **2**, 460-461.

The numbers of dead, oiled birds of each of fifteen species that were washed up on a stretch of seashore one mile long during 1951–53 are listed. Four waders probably became accidentally covered with oil after death. Diving birds appear to be most affected, since the low density of the oil prevents them from diving for food as well as from flying.

Harrison, R. J. (**1955**). Adaptations in diving mammals. *Sci. News*, **35**, 74-90.

Reviews some recent work, especially the peculiarities of the venous system.

Newell, G. E. (**1955**). Animal zones of the north Kent coast. *S.-East Nat.* **59** (1955), 34-56.

Discusses the animal life of the main intertidal zones of the coast near Whitstable.

Vevers, H. G. (1954). Photography of the sea floor. *New. Biol.* **17,** 91-95.

Describes apparatus developed at Plymouth, and its use in estimating the numbers of benthic organisms.

Wiseman, J. D. H. (1955). Marine organisms and biogeochemistry. *Nature, Lond.* **176,** 818-819.

An account of papers read at the British Association session on the above.

Woodhead, P. M. J. & Woodhead, A. D. (1955). Reactions of Herring larvae to light: a mechanism of vertical migration. *Nature, Lond.* **176,** 349-350.

Larvae of *Clupea harengus* were studied. These were dark adapted and then observed in different light intensities in shallow dishes illuminated from below. The activity of the larvae was found to be proportional to the light intensity between limits (20-4000 m-candles). The time spent moving during the fifteen minutes of observation was taken as a measure of the activity. Later experiments employed a tall glass cylinder. The positive photo ortho-kinesis persisted in this apparatus. The time spent swimming vertically and horizontally were recorded. Having reached a threshold level of light intensity by swimming vertically the larvae will swim increasingly in an horizontal direction, until the passive sinking is just counter-balanced. Theoretical consequences are discussed.

(*b*) Fresh Water

Bensley, C. J. F. (1955). The fresh-water Mollusca of the bomb-craters and gun-pits on Bookham Common. *Lond. Nat.* **34** (1954), 22-28.

An account of colonization by fresh-water molluscs, with some reference to insects and land molluscs, and a discussion of their source of origin and the suitability of the habitats for them.

Galliford, A. L. (1955). Two lakes of Delamere Forest—an ecological contrast. *Proc. Lpool Nat. Fld Cl.* **1954,** 21-26.

Compares the Rotifera and Cladocera of Hatch Mere (neutral) and Oak Mere (acid), the two largest bodies of water in the Forest.

Hinton, H. E. (1954). On the structure and function of the respiratory horns of the pupae of the genus *Pseudolimnophila* (Diptera: Tipulidae). *Proc. R. Ent. Soc. Lond.* (A) **29,** 135-140.

The respiratory horn acts as an automatic trapping device which tends to prevent the pupa from floating freely and results in bringing it against a bank from where it can wriggle ashore.

Lansbury, I. (1955). Some notes on invertebrates other than Insecta found attached to water-bugs (Hemipt.-Heteroptera). *Entomologist,* **88,** 139-140.

Records of Ostracods (*Cyclocyprinus ovum*) attached to the swimming hairs of *Notonecta obliqua* and *N. glauca* in Essex, *Pisidium* attached to the anterior palae of *Corixa punctata* in Herts, and a heavy infestation of Hydrachnids on *Sigara stagnalis* in Kent.

Leston, D. (1955). Miscellaneous biological notes on British Corixidae and Notonectidae (Hem.). *Ent. Mon. Mag.* **91,** 92-95.

Includes a comparison of the number of species present in eight ponds in August 1946 and March 1954, observations on the sex ratios of six species in the field, and on oviposition dates, reactions to light and other environmental conditions of adults and embryos, and stridulation in several species in aquaria. Overwintered Corixids with mites attached to the abdominal terga began to die off in spring earlier than others without them and it is concluded that the presence of the mites interferes with the dorsal air film.

Macan, T. T. (1955). The water bugs: a study in adaptation. *Discovery,* **16,** 75-79.

Summarizes the classification of water bugs as ecological groups, with particular reference to the Corixidae (cf. Macan, *J. Anim. Ecol.* **23,** 115-141).

(*c*) LAND

Bennett, S. H. (1955). The biology, life-history and methods of control of the leaf curling plum aphid *Brachycaudus helichrysi* (Kltb.). *J. Hort. Sci.* **30,** 252-259.

Diagnostic morphological features of various stages of the aphid, and its life-history on damson.

Blezard, E. (1955). Vertical range of snails. *Northw. Nat.* (N.S.) **3,** 255-256.

Records for several species in northern England, mostly at altitudes of 1000-2500 ft.

Bowen, E. G. (1955). Nature study and geography in West Wales. *Nature in Wales,* **1** (1), 17-21.

A general discussion based on average floral isophenes for the years 1891 to 1925, and on migrant isophenes for 1926 based on twenty species of birds.

Bramhill, R. (1955). Some observations on a family of foxes. *Naturalist,* **1955,** 13-15.

Daily observations at a Yorkshire fox set in June.

Brownsey, B. W. & Peakall, D. B. (1955). Jackdaw roost continuing throughout breeding season. *Brit. Birds,* **48,** 371.

In this instance the roost was a carrion crow roost, and used by jackdaws in spring and summer only, their winter roost being with rooks.

Burton, J. F. (1955). The butterflies of the north-west Kent marshes with special reference to the 1953 floods. *Lond. Nat.* **34** (1954), 54-60.

Information on habitats, distribution, abundance and, for some of the twenty-three species recorded, effects of severe floods in 1953, with a table showing in which of six habitats in the area each species commonly or probably breeds. Thames-side pasture and the earthen river walls were the habitats most affected by the floods. Comparative data for the thirteen species that normally pass all stages in the flooded area indicated that six were markedly reduced in 1953 and five were unaffected; the data for the other two were inconclusive. A flourishing colony of *Orthetrum cancellatum* appears to have been wiped out.

Clarke, J. R. (1955). Influence of numbers on reproduction and survival in two experimental vole populations. *Proc. Roy. Soc.* (B) **144,** 68-85.

Weekly censuses of two populations of *Microtus agrestis*, kept in large outdoor cages, were made for a total of eighteen months and the populations compared (growth rates, size, survival rates, fertility, length of breeding season). Aggressive activity and wounds (caused by other voles) were thought to be more frequent in the larger group: it is suggested that fighting restrained the growth of both populations, its effect being more severe in the larger group.

Cloudsley-Thompson, J. L. (1955). The biology of woodlice. *Discovery,* **16,** 248-251.

Habitats of several British species of the Isopoda are described. *Ligia oceanica* will withstand immersion in seawater; *Platyarthrus hoffmannseggi* is associated with the nests of ants and the burrows of wood-boring beetles; *Armadillidium vulgare* favours calcareous soils.

Collingwood, C. A. (1955). The glasshouse red spider mite on blackcurrants. *Ann. Appl. Biol.* **43,** 144-147.

The host-plant range of *Tetranychus urticae* is very wide, but the occurrence of the mite as a pest of blackcurrants appears to be related to the effects of modern insecticides upon its predators. Although in the glasshouse there may be ten generations each year, only four or five have been noted outdoors on currant.

Collyer, E. (1953). Biology of some predatory insects and mites associated with the fruit tree red spider mite (*Metatetranychus ulmi* (Koch)) in south-eastern England. II. Some important predators of the mite. *J. Hort. Sci.* **28,** 85-97.

Of forty-five species of insects and mites that feed on *M. ulmi*, detailed life-histories and

habits are given of those abundant in commercial orchards: *Anthocoris nemorum, Orius majusculus, O. minutus, Campylomma verbasci, Conaentzia pineticola, Oligota flavicornis, Stethorus punctillum, Typhlodromus tiliae, T. finlandicus* and *Phytoseius spoofi*.

Collyer, E. (1953). Biology of some predatory insects and mites associated with the fruit tree red spider mite (*Metatetranychus ulmi* (Koch)) in south-eastern England. III. Further predators of the mite. *J. Hort. Sci.* **28,** 98-113.

Predators of *M. ulmi* which are not abundant in commercial orchards are described. Twelve species of the family Miridae (Hemiptera-Heteroptera) are considered, and details given of their immature stages. Also noted are Thysanoptera, Hemiptera-Heteroptera (Nabidae), Neuroptera (Chrysopidae and Hemerobiidae), Diptera (Syrphidae) and Acarina.

Collyer, E. (1953). Biology of some predatory insects and mites associated with the fruit tree red spider mite (*Metatetranychus ulmi* (Koch)) in south-eastern England. IV. The predator-mite relationship. *J. Hort. Sci.* **28,** 246-259.

Compares predator populations in unsprayed, neglected orchards and in commercial orchards, with reference to their effects on *M. ulmi*. Includes the effect of predators on winter eggs of the mite.

Condry, W. (1955). Breeding birds of the Welsh mountains. *Nature in Wales,* **1** (1), 25-27.

Ecological notes on the typical mountain species of Wales.

Coombs, C. W. & Freeman, J. A. (1955). The insect fauna of an empty granary. *Bull. Ent. Res.* **46,** 399-417.

Gives full history of large granary in a dock area; boarded-up cavities in walls contained grain residues and numerous (average 266 insects per foot of wall) storage pests (thirty-four species identified). The absence of eight species known to have been present at an earlier date is discussed.

Corbet, P. S. & Tjønneland, A. (1955). Rhythmic flight activity of certain East African Trichoptera. *Nature, Lond.* **175,** 1122-1123.

Using a Robinson-type insect trap, from which the catch was removed at ten-minute intervals, a bimodal nocturnal activity is shown in the Ephemoptera, Trichoptera and Chironomidae. The peaks of activity are after sunset and before dawn. Seven species of Trichoptera showed this clearly, the dawn activity being great but short-lived in six of these. It is suggested that sexual activity is greatest at this latter time. The studies should lead to economy of effort in further work.

Cott, H. B. (1953, 1954). The exploitation of wild birds for their eggs. *Ibis,* **95,** 409-449, 643-675; **96,** 129-149.

The estimated annual egg crop of all species of wild birds in the world whose eggs are commonly exploited by man is tabulated, and the effects, past and present, on populations are reviewed.

Cramp, S. (1955). The breeding of the willow warbler. *Bird Study,* **2,** 121-135.

A compilation from nest record cards of the B.T.O. from 1939 to 1952, supplemented by other records. The breeding season in Great Britain lasts from late April to early July, the peak being in the second half of May. It tends to fall one week later in the north than in the south-east and south-west. Probably between 5 and 10 per cent of birds are double brooded. Average clutch-size is just over six, being at a maximum in mid-May and slightly higher in the north than in the south. Incubation period is 13 days, nestling period 13·2 days. Only about 7 per cent of nests were over 1 ft above ground, the highest being at 8 ft. As a consequence of this greater susceptibility to predators, although hatching success is high, nestling success is relatively low.

Cramp, S. & Teagle, W. G. 1955. A comparative study of the birds of two stretches of the Thames in Inner London, 1951-53. *Lond. Bird. Rep.* **18** (1953), 42-57.

The data obtained from counts of the gulls and other birds on two reaches providing somewhat different conditions made weekly throughout 1951-53 are given in tables and compared with similar data for gulls during 1931-32. Histograms show the average monthly abundance in 1951-53 of great and lesser black-backed, herring, common and black-headed gulls and of mute swans and feral pigeons in each reach, and the observed seasonal trends and feeding and other habits of these birds and of mallard, carrion crow and house sparrow are discussed and in some cases compared with behaviour in other towns. All the gulls have increased in abundance since the earlier counts, and this trend is most marked in the larger gulls, especially the great black-backed, which are also present in more months in the year than formerly.

Dowdeswell, W. H. & Ford, E. B. 1955. Ecological genetics of *Maniola jurtina* L. on the Isles of Scilly. *Heredity*, **9**, 265-272.

The female spot-distribution of the meadow brown butterfly in the Isles of Scilly is maintained at distinct, constant values, by selection, in different islands and parts of islands. A change of conditions, such as for instance the removal of cattle from Tean, which allowed a short-cropped turf barrier between two distinct local populations to grow long, may change the spot-distribution in small areas.

Downes, J. A. 1955. Observations on the swarming flight and mating of *Culicoides* (Diptera: Ceratopogonidae). *Trans. R. Ent. Soc. Lond.* **106**, 213-236.

Swarms, usually almost entirely of males, occur in a number of named *Culicoides* species (and other Ceratopogonidae) and are related to a distinct object, the swarm-marker. The swarm-marker is recognized visually and each individual responds to the marker independently. No swarm consists of more than one species and the markers are specific. Observations suggest that females respond to the male swarm-marker, fly into the swarm and mate. Swarming therefore brings the sexes into close proximity and perhaps functions as an isolating mechanism. Mating is brought about within the swarm, by the auditory recognition of the flying female by the male; it is likely that this recognition is non-specific. *Culicoides nubeculosus*, *C. riethi* are able to mate while at rest and non-specific recognition depends on contact.

Dunn, J. A. & Wright, D. W. 1955. Population studies of the pea aphid in East Anglia. *Bull. Ent. Res.* **46**, 369-387.

Acyrthosiphon pisum populations studied on several leguminous crops over four years. Weather effects were more severe than biological agents in reducing populations.

Dunn, J. A. & Wright, D. W. 1955. Overwintering egg populations of the pea aphid in East Anglia. *Bull. Ent. Res.* **46**, 389-392.

Mortality of winter eggs on hop trefoil was greater than on lucerne.

Edney, E. B. 1954. Woodlice and the land habitat. *New Biol.* **17**, 41-57.

Fenner, F. & Marshall, I. D. 1955. Occurrence of attenuated strains of myxoma virus in Europe. *Nature, Lond.* **176**, 782-783.

Gives a standard technique for the comparison of the virulence of myxoma strains and reports cases of attenuated strains which it is suggested will replace the virulent strains where the two come into competition.

Forster, G. H. 1955. Thermal air currents and their use in bird-flight. *Brit. Birds* **48**, 241-253.

The conditions for the existence of ascending air currents are described and some instances of their deliberate use by birds are given. Cumulus clouds indicate the existence of thermals.

Gillett, J. D. 1955. Behaviour differences in two strains of *Aëdes aegypti*. *Nature, Lond.* **176**, 124-125.

Strains from Lagos, Nigeria and Newala, Tanganyika, show different hatching responses

in the eggs. Further differences in the adults—Lagos strain unmated females usually lay eggs within five days of taking a blood meal, Newala strain rarely within this period. Mating experiments are described. It is suggested that the females of the Lagos strain produce some substance that stimulates ovulation and that extra production of this follows impregnation by the male. This substance is wanting in Newala strain but appears about two days after impregnation.

Haig-Thomas, P. (1955). *Adopoea lineola* unaffected by floods. *Entomologist,* **88,** 83.

This butterfly was as common in July 1954 in Horsea Island, Essex, which was submerged for several days and, in parts, for a month early in the year, as before the flooding. *Maniola jurtina* and *Epinephele tithonus* were very scarce, *Polyommatus icarus* absent, and there were few *Pieris rapae* and *P. brassicae,* but *P. napi* was fairly common.

Hartland-Rowe, R. (1955). Lunar rhythm in the emergence of an ephemopteran. *Nature, Lond.* **176,** 657.

The dates of recorded swarms of *Povilla adusta* are compared with the occurrence of the full moon. A field experiment supports the theory that swarms only occur within five days of the full moon, and most usually two days after.

Holder, F. W. (1954). The flighting times of the pink-footed geese of Martin Mere, Lancashire. *Northw. Nat.* (N.S.) **2,** 559-563.

Almost daily records of the times of morning and evening flights between Martin Mere and the Ribble Estuary from 21 September 1953 till 22 March 1954.

Hudson, J. R., Thompson, H. V. & Mansi, W. (1955). Myxoma virus in Britain. *Nature, Lond.* **176,** 783.

Reports an attenuated strain from the Sherwood Forest area. More recent strains moving over the same area are more virulent. Immunity, built up by the former infection, will considerably reduce the mortality. The situation is being watched carefully.

Hughes, R. E. (1955). Ecology of Snowdonia. Ecology of livestock productivity. *Nature, Lond.* **176,** 595-596.

Jones, F. G. W., Dunning, R. A. & Humphries, K. P. (1955). The effects of defoliation and loss of stand upon yield of sugar-beet. *Ann. Appl. Biol.* **43,** 63-70.

Field trials with insect-simulated injury to sugar-beet seedlings showed that 50 per cent defoliation in the 4- or 8-leaf stage caused only 5 per cent decrease in root yield, and complete defoliation no more than 30 per cent decrease. Similarly, loss of half the plant population (as from the feeding of wireworms and millipedes) caused a reduction in root yield of 10 per cent. Good recovery can be expected from most pest attacks, few of which cause more than 50 per cent defoliation or loss of stand.

Kettle, D. S. (1955). Sex ratios among the British *Culicoides. Proc. R. Ent. Soc. Lond.* (A) **30,** 70-72.

The rearing of mature larvae produced the normal 1:1 sex ratio in the cases of twenty-six named species of British *Culicoides.* The unusual sex ratios obtained by sweep net, sticky trap or box trap collecting methods, therefore, requires some other explanation, such as differential activity or mortality.

Laurence, B. R. (1955). Flies associated with cow dung. *Ent. Rec.* **67,** 123-126.

Observations, mostly at Rothamsted, on the behaviour of flies, of various genera, with coprophilous larvae. Every degree of association with the herd was found from independence except for oviposition to dependence for adult food and habitat.

Lockley, R. M. (1955). The failure of myxomatosis on Skokholm Island. *Nature, Lond.* **175,** 906-907.

The absence of the rabbit flea is associated with the failure of myxomatosis. Skomer shows both flea and virus.

London Natural History Society (1955). Cranford Park Survey. *Lond. Nat.* **34** (1954), 42-43.

Contains a list of the birds that nested in or visited the park, by A. Anderson, and more detailed notes on the abundance of the thirteen mammals, one reptile and four amphibia noted there during 1950-54, by B. Coleman.

London Natural History Society (1955). The survey of Bookham Common. Thirteenth year. *Lond. Nat.* **34** (1954), 13-36.

An introductory progress report includes brief summaries of work in 1954 on Diptera and leaf-mining insects by L. Parmenter (pp. 14-15), the territories of wrens and yellow buntings and the winter movements of chaffinches by G. Beven (p. 15), and mammalian bones in pellets of tawny owls in a wood by G. Beven (p. 15). The Report also includes a paper on the vegetation of the bomb-crater ponds and gun-pits containing some information on the fauna, by C. P. Castell (pp. 16-21), one including a list of beetles found in the gun-pits in 1945-46 compiled by Castell from notes by the late L. G. Payne (pp. 21-22), one on the freshwater molluscs of the bomb-craters and gun-pits by C. J. F. Bensley (pp. 22-28), and a preliminary list of the Macro-lepidoptera recorded from the Common by A. S. Wheeler (pp. 28-36).

Mackenzie, J. M. D. (1954). Redstarts reared in tits' nests. *Scot. Nat.* **66,** 146-154.

Records a redstart, losing its own nest and three eggs, laying two eggs in the nest of a *Parus major*, followed by six more in that of a *P. ater*, the latter bird laying eleven eggs. Six redstarts and eight tits hatched. The redstart laid and reared four eggs more in a new nest. At least one redstart in the *P. major* nest and two in the *P. ater* flew. Neither colour, nor size of egg or clutch, nor differences in the nestlings' mouths affected the tits' parental reactions.

Melluish, W. D. (1955). Census of great crested grebes, 1953. *Lond. Bird Rep.* **18** (1953), 40-41.

The total number of adults in the London area in 1953 increased by nearly 17% and there were also increases in each of the six counties involved except Surrey, where there was a reduction of 28·8%. The greatest increases were in Middlesex (56%) and Essex (34%).

Melluish, W. D. (1955). The census of great crested grebes, 1954. *Lond. Bird Rep.* **19** (1954), 43-44.

The number of waters in the London area occupied by grebes increased to 105 in 1954, but the total number of adults declined by 5·9%, and a reduction occurred in all counties except Herts. Birds were most numerous on reservoirs and lakes, but gravel pits were preferred for breeding. The breeding status was maintained. The average number of birds per ten acres on fifty-one waters supporting breeding pairs, both breeding and non-breeding birds, and only non-breeding birds and corresponding broadly with the smaller gravel pits and lakes in parks, larger gravel pits and reservoirs with natural banks and cover, and larger reservoirs with concrete banks, was estimated at 1·35, 1·69 and 0·53% respectively. The average area of water available per adult in the three categories was 7·4, 5·9 and 18·8 acres respectively.

Nickerson, B. (1954). Insect pigments and coloration. *Sci. News,* **34,** 85-94.

A brief account of exogenous and endogenous pigments, and a short general review of their roles in insect coloration.

Owen, D. F. (1954). The winter weights of titmice. *Ibis,* **96,** 299-309.

1500 weights were obtained. *Parus major*, *P. ater* and *P. caeruleus* were on average heaviest in December, and thereafter weights gradually fell.

Phillips, W. M. (1955). The effect of commercial trapping on rabbit populations. *Ann. Appl. Biol.* **43,** 247-257.

The effect of trapping on two rabbit populations in western Wales was investigated from 1946 to 1949. Trapping removed 30-40 % of the population. Breeding was intense from January to June, and also in the autumn; the sex ratio varied around a mean of 50%. Data are given on movements, foraging range and life expectation.

Ribbands, C. R. (1954). The defence of the honeybee community. *Proc. Roy. Soc.* (B) **142,** 514-524.

Describes experiments with pairs of colonies (arranged with entrances 2 in. apart) of different coloured bees. The reception of bees attempting to enter the wrong colony varied with foraging conditions obtaining at the time. Discusses the results in relation to defence against robber bees and strange queens.

Sankey, J. (1955). The Long-tailed Field Mouse. *Oryx,* **3,** 102-103.

Discusses habits, breeding and economic significance of *Apodemus sylvaticus.*

Satchell, J. E. & Collingwood, C. A. (1955). The wood ants of the English Lake District. *Northw. Nat.* (N.S.) **3,** 23-29.

The results of a distribution survey in 1954, including tabulated data and a map, with isohyets, for *Formica rufa,* and discussions of its status and factors affecting its distribution. It is abundant in limestone woodland near Arnside and Grange-over-Sands, but scarce on Silurian formations near Windermere, where the number of colonies has declined, apparently owing to invasion of woodlands by bracken following extensive felling; three localities constituting its northernmost limit in Britain are given. *F. lugubris* occurs in two districts.

Savory, T. H. (1954). Scorpions in Britain. *Discovery,* **15,** 233-235.

An informative, popular account of the Chelonethi, with notes on their food requirements and conditions for keeping them alive for study.

Snow, D. W. (1954). The habitats of eurasian tits (*Parus* spp.). *Ibis,* **96,** 565-585.

Several species, including British species, occupy atypical habitats in limited areas of their geographical range. The role of competition in the evolution of preferences is considered.

Snow, D. W. (1955). The breeding of the blackbird, song thrush and mistle thrush in Great Britain. II. Clutch size. *Bird Study,* **2,** 72-84.

In the blackbird and song thrush mean clutch size varies seasonally, reaching a peak in the third week of May and the end of April/beginning of May respectively. The annual variations for the two species show some parallelism, which may be correlated with temperature. In the north, clutch size is lower than in southern England at the beginning of the season, but higher at the end.

Solomon, M. E. & Adamson, B. E. (1955). The powers of survival of storage and domestic pests under winter conditions in Britain. *Bull. Ent. Res.* **46,** 311-355.

Of sixty-eight species of insect pest exposed in unheated outbuildings for one or more winters, nearly half survived the severest tests. Survival of several species differed from results of earlier workers.

Southern, H. N. (1955). A Britain without rabbits? *Discovery,* **16,** 186-189.

Considers some of the ecological consequences of the reduction of the rabbit population by the spread of myxomatosis. Covers not only the effects on grassland, crops and woodland, but also draws attention to probable food-chain disruptions and to the possible extension of grazing by other herbivores.

Thomas, D. C. (1955). Notes on the biology of some Hemiptera Heteroptera. III. Neididae. *Entomologist,* **88,** 89-91.

Notes on the occurrence of *Neides tipularius* and ten other species in very great numbers and eighteen others in less abundance in an old *Brassica* seed-bed overgrown with weeds in South Devon, and on the food-plants, distribution and life-cycles of *Berytinus crassipes, B. hirticornis,* and *Metatropis rufescens.*

Thomas, D. C. (1955). Notes on the biology of some Hemiptera Heteroptera. IV. Lygaeidae. *Entomologist,* **88,** 145-152.

Notes on the habitats, food, abundance and bionomics of eleven species, with descriptions of the eggs.

N J.A.E.

Tutt, H. R. (1955). Observations on a pair of nightjars at the nest. *Brit. Birds,* **48,** 261-266.

Urbain, A. & Nouvel, J. C. G. (1954). On keeping wild animals in zoos. *Endeavour,* **13,** 184-189.

Discusses the zoo as a special type of habitat, and the proposition that the natural state is not one of freedom, since animals in the wild are restricted in their movements by very many factors. Problems of diet, pathology and the study of behaviour are also mentioned.

Warham, J. (1955). The blue tit's year. *New Biol.* **19,** 70-80.

Waterhouse, F. L. (1955). Microclimatological profiles in grass cover in relation to biological problems. *Quart. J. Roy. Met. Soc.* **81,** 63-71.

Air temperatures, relative humidities and wind speeds were estimated, using thermo-junction equipment, in grass stands in Angus. The climatic conditions recorded are analysed and discussed in relation to the effects of grass cover on insect life.

Williams, C. B. (1955). Phenology — the study of the changing seasons in biology. *Countryside,* **17,** 236-239, 278-279.

Extracted from the Presidential Address to the Assembly of Corresponding Societies of the British Association delivered at Oxford in 1954.

Yapp, W. B. (1955). The succession of birds in developing *Quercetum petraeae*. *Northw. Nat.* (N.S.) **3,** 58-67.

Bird populations in three areas in Wyre Forest representing stages in the development of high oak (*Q. petraea*) forest from oak-birch scrub were studied by means of line transects during April-June and October-March 1953, and the data obtained are given in tables and discussed. As the sere developed, the number of bird species and over-all densities increased and there was an increase in the number and variety of niches rather than a replacement of one set by another.

Yapp, W. B. (1955). A classification of the habitats of British birds. *Bird Study,* **2,** 111-121.

A comprehensive classification of the broad features of all potential habitats of interest to birds in Britain. Principally of use in recording ornithological data, but can be useful as a beginning in the study of the ecology of other animals.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Axell, H. E. (1955). The 'Dungeness' ringing pliers. *Brit. Birds,* **48,** 229.

An aid to quick bird ringing, illustrated.

Brownlow, H. G. (1955). Reconstruction of Heligoland traps. *Bird Study,* **2,** 86-87.

Notes on methods of preventing and repairing damage to traps.

Cloudsley-Thompson, J. L. (1955). The design of entomological aktograph apparatus. *Entomologist,* **88,** 153-161.

A descriptive review of various types of apparatus that have been devised by investigators for determining the effect of environmental conditions on the activity of animals.

Coombs, C. W. & Woodroffe, G. E. (1955). A revision of the British species of *Cryptophagus* (Herbst) (Coleoptera: Cryptophagidae). *Trans. R. Ent. Soc. Lond.* **106,** 237-282.

Includes keys to the subgenera of *Cryptophagus*; the species of *Cryptophagus* s.str., *Micrambe* and *Micrambe*. Gives notes on the British species of these genera.

Doull, K. M. (1955). An electrified barrier for caterpillars. *Nature, Lond.* **176,** 842.

Describes an apparatus suitable for caging small caterpillars in the laboratory.

Foster, F. G. (1955). A note on Bailey's and Whittle's treatment of a general stochastic epidemic. *Biometrika,* **42,** 123-125.

A new general formula for calculating the probabilities of possible total sizes of an epidemic.

Godfrey, G. K. (1955). Radioactive tagging of small animals. *Discovery,* **16,** 320-322.

A synopsis of papers already published in *Ecology* and elsewhere.

Gray, P. H. H. (1955). An apparatus for the rapid sorting of small insects. *Entomologist,* **88,** 92-93.

Devised for the separation of Lepidoptera and Coleoptera from large catches of small insects in a funnel-trap to which they were attracted by an ultra-violet lamp.

Gulland, J. A. (1955). On the estimation of population parameters from marked members. *Biometrika,* **42,** 269-270.

Assumes that the probability of an individual being alive at time t is $e-(F+M)t$, where F represents the losses from fishing and M the rest of the mortality. If N individuals are released and n recaptured on a total of r separate occasions, $\hat{F} = n^2/Nr$ and $\hat{M} = (N-n)n/Nr$ are biased estimates which may prove reasonable in practice if large numbers are involved, and if the observations continue until none of the original animals are likely to be still alive.

Gulland, J. A. (1955). Estimation of growth and mortality in commercial fish populations. *Fish. Invest., Lond.* (2)**18**(9), 1-46.

Mathematical and statistical methods which enable the composition of the natural population, and, as far as possible, accurate and unbiased estimates of growth rates and mortality to be deduced from landings. The theoretical methods are tested against North Sea catches of plaice and other fish.

Habib, A. (1955). On the species of *Eulecanium* Ckll. (Homoptera, Coccoidea, Coccidae) on *Taxus baccata* L. *Ent. Mon. Mag.* **91,** 70-72.

The Coccid on *T. baccata* hitherto known as *E. corni* var. *crudum* is here stated to represent a new species, designated *E. taxi*. Characters separating the larvae and adults of both sexes from those of *E. corni* are given.

Haldane, J. B. S. (1955). Population genetics. *New Biol.* **18,** 34-51.

An introduction to the subject.

Henson, H. (1955). On *Hydrobaenus ephemerae* (Kief.). Chironomidae: Diptera. *Entomologist,* **88,** 131-136.

Contains detailed descriptions and figures of the larva, pupa and adult of this Chironomid, which is phoretic on nymphs of *Ephemera danica*, with some information on its bionomics.

Hewer, H. R. & Neal, E. G. (1954). Filming badgers at night. *Discovery,* **15,** 121-124.

For successful cinematography, badgers were conditioned over a period of several months to artificial lighting and the noise of the camera. These disturbances were associated with the presentation of food in the case of a set where the badgers were accustomed to feeding on dustbin scraps.

Hickin, N. E. (1954). Larvae of the British Trichoptera.—46. *Proc. R. Ent. Soc. Lond.* (A) **29,** 145-146.

The larva of *Micropterna lateralis* is described and figured and a figure of the adult is given.

Hickin, N. E. (1954). Larvae of the British Trichoptera.—47. *Proc. R. Ent. Soc. Lond.* (A) **29,** 153-155.

The larva of *Triaenodes conspersa* is described and figured and a figure of the adult is given.

Hickin, N. E. (1954). Larvae of the British Trichoptera.—48. *Proc. R. Ent. Soc. Lond.* (A) **29,** 172-173.

The larva of *Crunoecia irrorata* is described and figured and a figure of the adult is given.

Hickin, N. E. (1954). Larvae of the British Trichoptera.—49. *Proc. R. Ent. Soc. Lond.* (A) **29,** 174-176.

The larva of *Trichostegia minor* is described and figured and a figure of the adult is provided.

Hickin, N. E. (1955). Larvae of the British Trichoptera.—50-51. *Proc. R. Ent. Soc. Lond.* (A) **30,** 55-58.

The larvae of *Phryganea obsoleta* and of *P. striata* are described and figured. The adults are also figured.

Hughes, R. E. & Lindley, D. V. (1955). Application of biometric methods to problems of classification in ecology. *Nature, Lond.* **175,** 806-807.

Discusses a multivariate analysis technique based on the statistic D^2, calculated from the means, variances and covariances of the quantities measured in two groups. D^2 being greater the larger the differences between the groups. It is a measure of the 'distance' between the two groups. The D^2s of different pairs may be compared. The method is illustrated by the analysis of the characteristics of six Snowdonian soil series. Applications of these methods are suggested.

Johnson, A. L. (1955). Seal catching. *Nature in Wales,* **1** (2), 54-56.

Lessons in seal catching learned during the marking of grey seal pups by clipping numbered metal rings on the rear flippers.

Johnson, C. G., Southwood, T. R. E., & Entwhistle, H. (1955). A method for sampling arthropods and molluscs from herbage by suction. *Nature, Lond.* **176,** 559.

The apparatus basically an electric blower. Figures suggesting a high efficiency are given.

Kettlewell, H. B. D. (1955). Labelling locusts with radio-active isotopes. *Nature, Lond.* **175,** 821-822.

Laboratory experiments are described, and subsequent observations recorded. The method may be very useful in marking the hopper stages, but seems to have no advantage over the colour paints in the adults.

King, J. M. B. (1954). Some experiments in trapping wading birds. *Northw. Nat.* (N.S.) **2,** 377-383.

An account of attempts to trap waders in the Hilbre-Hoylake area with clap traps, which were too slow in action, funnel traps, which were too laborious for the results achieved, and clover-leaf traps, which were moderately successful on seaweed-covered rocks. With these three traps, seventeen oystercatchers, ten turnstone, two redshank and one purple sandpiper were trapped on fifteen expeditions.

Legg, J. T. (1955). A combined aspirator and feeding cage for the collection and testing of insects as vectors of plant viruses. *Nature, Lond.* **176,** 609.

Mackereth, J. C. (1954). Taxonomy of the larvae of the British species of the genus *Rhyacophila* (Trichoptera). *Proc. R. Ent. Soc. Lond.* (A) **29,** 147-152.

Includes a key to the fully grown larvae of *R. munda, R. obliterata, R. dorsalis* and *R. septentrionis.*

Marler, P. (1955). Characteristics of some animal calls. *Nature, Lond.* **176,** 6-8.

Sound spectrographs of various bird calls are given, and these are correlated with behaviour patterns. Concerns particularly predator-prey relations.

O'Connor, F. B. (1955). Extraction of enchytraeid worms from a coniferous forest soil. *Nature, Lond.* **175,** 815-816.

A wet funnel technique is described in detail, and results are considered.

Rushton, S. & Mautner, A. J. (1955). The deterministic model of a simple epidemic for more than one community. *Biometrika,* **42,** 126-132.

Gives a general solution and discusses in detail the case in which the epidemic starts with but one infected individual.

Skellam, J. G. (1955). Quadrat sampling from the mathematical standpoint. *Proc. Linn. Soc. Lond.* **165,** 95-102.

A largely pictorial discussion of some points considered by the author in *Biometrika,* **39,** 346-362 (1952). See *J. Anim. Ecol.* **22,** 393 (1953).

Southern, H. N. (1955). The study of British mammals. *Countryside,* **17,** 231-235.

Distribution, methods of study and key to identification of small mammal skulls in owl pellets.

Svendson, J. A. (1955). Earthworm population studies: a comparison of sampling methods. *Nature, Lond.* **175,** 864.

The permanganate method of sampling is found to give a low population estimate when compared with results obtained by hand sampling. Moreover the former has differing effects on the species investigated. It might be used to determine differences in habits of the species.

Thompson, H. R. (1955). Spatial point processes, with applications to ecology. *Biometrika,* **42,** 102-115.

The analysis of the distribution of numbers of individuals in a rectangular grid. The mathematical theory is discussed in detail; particular cases of interest to ecologists will be discussed elsewhere.

Whittle, P. (1955). The outcome of a stochastic epidemic—a note on Bailey's paper. *Biometrika,* **42,** 116-122.

A new method for calculating the probability of the total size of an epidemic. In some cases a stochastic equivalent of the threshold phenomenon can be found.

Wynne, O. E. (1953-55). Key-list of the palaearctic and oriental passerine birds. *Northw. Nat.* (N.S.) **1,** 580-597; **2,** 123-137, 297-319, 436-459, 619-647; **3,** 104-128.

Wynne-Edwards, V. C. (1955). The dynamics of animal populations. *Discovery,* **16,** 433-436.

An essay review of D. Lack, 1954, *The natural regulation of animal numbers,* Oxford. The implication that natural selection cannot favour a smaller egg-number as such may be fallacious as the most fecund are not necessarily the fittest.

3. PARASITES

Arthur, D. R. (1955). New species of ticks (Ixodes) associated with small mammals. *Parasitology,* **45,** 131-140.

Describes a new species, *Ixodes thompsoni,* recovered from a cat on Lundy Island, a new species, *Ixodes guerneseyensis,* harboured by *Evotomys glareolus* from the Channel Isles, as well as a new variety of *Ixodes arvicolae* found in a mouse's nest from North Zealand, Denmark.

Ash, J. S. (1955). Some records of bird and mammal ectoparasites. *Ent. Mon. Mag.* **91,** 64-65.

Records of Hippoboscids, Nycteribiids, Ceratophyllids and Cimicids on twenty-three birds, Daubenton's bat and man in Hants., Dorset, Northumberland and Sweden, with dates and the number and sexes of the parasites.

Chambers, V. H. (1955). Some hosts of *Anteon* spp. (Hym., Dryinidae) and a hyperparasite *Ismarus* (Hym., Belytidae). *Ent. Mon. Mag.* **91,** 114-115.

A. flavicorne and its variety *bensoni* emerged on 11 May and 1 June respectively, from nymphs of *Idiocerus* associated with adults of *I. laminatus* and *I. populi* and unparasitized nymphs of *I. populi* on *Populus tremuli*. *A. brachycerum* emerged on 10 May from nymphs of *Oncopsis* on *Betula*. *Ismarus flavicornis* parasitized *A. flavicorne* in 1952 and this constitutes the first record of a host for the former and a hyperparasite of the latter; *I. halidayi* was reared from *A. brevicorne* parasitic in nymphs of *Oncopsis* associated with adults of *O. flavicollis* and unparasitized nymphs of *O. tristis*.

Corbett, M. P. (1955). Occurrence of two species of *Crepidostomum* in brown trout (*Salmo trutta* L.) from north-east Ireland with special reference to *Crepidostomum metoecus* Braun 1900. *Parasitology,* **45,** 186-188.

Two species of *Crepidostomum* were found during a study of the helminth parasites of the local freshwater fish in north-east Ireland. The source of *Crepidostomum metoecus*, which is said to be a parasite of noctule bats, is discussed.

Crofton, H. D. (1955). Nematode parasite populations in sheep on lowland farms. II. Worm egg counts in lambs. *Parasitology,* **45,** 99-115.

Cutcliffe, A. S. (1955). Further notes on the swift, 1944-54. *Brit. Birds,* **48,** 193-203.

Includes notes on parasites. (See also Cutcliffe, A. S., 1951, *Brit. Birds,* **44**, 47-56 and 176-177. Abstracts in 1955, *J. Anim. Ecol.* **24,** 214 and 215.)

Gotto, R. V. (1955). A note on the ecology of the genus *Lichomolgus* (Copepoda: Cyclopoida). *Ann. Mag. Nat. Hist.* (12) **8,** 390-392.

Semi-parasites or commensals of molluscs and ascidians. Possibly some species, when adult, leave the host.

Jennings, A. R. (1955). Diseases in wild birds. *Bird Study,* **2,** 69-72.

Summarizes autopsy results on 224 wild birds over a period of three years. Where cause of death could be determined, bacterial and virus infections were operative in thirty-six and thirty-four cases respectively. Injury and chemical poisoning accounted for sixty-nine other birds.

Kettle, D. S. & Utsi, M. N. P. (1955). *Hypoderma diana* (Diptera, Oestridae) and *Lipoptena cervi* (Diptera, Hippoboscidae) as parasites of reindeer (*Rangifer tarandus*) in Scotland with notes on second-stage larva of *Hypoderma diana*. *Parasitology,* **45,** 116-120.

Imported reindeer have become infested with parasites—the deer ked and the deer warble, which they acquired from local deer. In their native haunts reindeer harbour their own warble (*Hypoderma tarandi*), but steps were taken to ensure that this parasite was not introduced into Scotland; the first consignment was treated with derris root and the warbles were hand picked from the animals in the second batch. The reindeer probably acquired their warbles *H. diana* from the red-deer in Scotland. Keds are not usually found on reindeer in N. Scandanavia, but are found on roe-deer, red-deer, elk and sika-deer. The absence of deer ked on reindeer in their native habitat may be due to the fact that no species of *Lipoptena* is known to occur above 60° N.

Lal, Makund Behari (1955). Occurrence of a new parasite (*Trematode metacercaria*) in the eyes of Scottish Trout. *Proc. R. Phys. Soc. Edinb.* **24** (1), 1-3.

Gives table of incidence in *Salmo trutta* populations from various bodies of water. Infection heavier in lochs and reservoirs than in rivers.

Lockley, R. M. (1955). Observations on myxomatosis in Wales in 1954. *Nature in Wales,* **1** (2), 57-62.

A summary of a report submitted to the Nature Conservancy. Deals with ectoparasites, human and other agencies of spread, rate of natural spread, duration and lethality of epidemics, effects on other animal species and flora, etc.

Naylor, E. (1955). The seasonal abundance on *Idotea* of the cocoons of the flat worm *Plagiostomum oyense* de Beauchamp. *Rep. Port Erin Mar. Biol. Sta.* **67,** 25-30.

Gives details of the incidence of the cocoons of *P. oyense* on *Idotea* spp. at Port Erin and relates the degree of infection to the size of the host. The monthly variation in numbers and condition of the cocoons is given.

Owen, D. F. (1955). Additional records of *Protocalliphora* (Diptera) in birds' nests. *Brit. Birds,* **48,** 225-229.

(See also Owen, D. F., 1954, *Brit. Birds,* **47**, 236-243. Abstract in 1955, *J. Anim. Ecol.* **24,** 485.)

Smith, K. G. V. (1955). Further notes on Acari in association with *Limonia tripunctata* F. and other Tipulidae (Dipt.). *Ent. Mon. Mag.* **91,** 51-52.

The percentage infestation of *L. tripunctata* by ectoparasitic larval mites of the genera *Calyptostoma* and *Johnstoniana* amounted to 20, 9 and 4 on 24 May and 3 June 1951, and 24 May 1952, respectively, in one wood in Shropshire and 60 on 17 June 1951, in another. *Calyptostoma* and *Johnstoniana* occur together in a similar locality; the former was virtually confined to the thoracic region of the host and the latter to the abdomen, where about 75% were on the first two segments. Larval *Johnstoniana* were also taken on *L. macrostigma,* where they were also confined to the abdomen, and *Tipula luna,* where they were on the thorax and may represent a different species.

Smith, K. G. V. (1955). Notes on some Acarine ectoparasites of Diptera. *Ent. Mon. Mag.* **91,** 141.

Records of the occurrence of mites on flies of seven families.

Smith, K. M. (1954). Viruses and the control of insect pests. *Discovery,* **15,** 455-458.

This general statement includes more detailed information on trials with a polyhedral virus isolated from *Vanessa cardui* and used against larvae of *Bupalus piniarius* and *Operophtera brumata.* The virus caused total kills of *O. brumata* and high mortality of *B. piniarius,* but no natural virus disease was observed in these species.

Stoker, M. G. P., Brown, R. D., Kitt, F. J. L., Collings, P. C. & Marmion, B. P. (1955). Q fever in Britain: isolation of *Rickettsia burneti* from placenta and wool of sheep in an endemic area. *J. Hyg., Camb.* **53,** 313-321.

Rickettsia burneti was isolated from two out of ninety-six placentas from 118 ewes in one flock and from the wool tags from one of the ewes with an infected placenta.

Stoker, M. G. P. & Marmion, B. P. (1955). Q fever in Britain: isolation of *Rickettsia burneti* from tick *Haemaphysalis punctata. J. Hyg., Camb.* **53,** 322-327.

Distribution of ticks in the British Isles is discussed, the sheep tick *Ixodes ricinus* is the only tick which is common and widely distributed, but *Haemaphysalis punctata* is common in Kent, to the exclusion of *Ixodes ricinus.* The organism responsible for Q fever (*Rickettsia burneti*) has been isolated from *H. punctata* collected from sheep in an endemic area in Kent.

Taylor, E. (1955). *Phyto melanocephala* Meig. (Dipt., Tachinidae) bred from *Armadillidium vulgare* (Latr.) (Oniscoidea). *Ent. Mon. Mag.* **91,** 72.

This Tachinid is known to parasitize *Porcellio scaber* and *Oniscus asellus*, but its relationship with *A. vulgare* was hitherto confused.

Thompson, G. B. (1955). The parasites of British birds and mammals. - XXVIII. Records of *Ornithomyia* spp. (Dipt., Hippoboscidae) collected during 1952. *Ent. Mon. Mag.* **91,** 4-5.

A list of the hosts of thirty-two *O. fringillina* and three *O. avicularia* taken at bird observatories during 1952 with dates and the place of capture, and another of records of puparia of these two species found in birds' nests.

Thompson, G. B. (1955). The parasites of British birds and mammals.—XXIX. Some interesting records of bird-fleas (Siphonaptera). *Ent. Mon. Mag.* **91,** 43-45.

A list showing the numbers and sexes of *Ceratophyllus gallinae*, *Dasypsyllus gallinulae* and *C. garei* found on the bodies of resident and migrant birds, with the circumstances of capture and notes on the occurrence of six fleas found in birds' nests.

Thompson, G. B. (1955). Ectoparasites from Skokholm Bird Observatory. *Nature in Wales,* **1** (3), 128-130.

Representatives of four groups of ectoparasites—bird-flies and fleas, bird-lice and ticks - were obtained in 1954 from sixteen different species of birds.

Wilkinson, P. R. (1955). Temporary destocking of pastures to aid control of the cattle tick. *Nature, Lond.* **176,** 515.

A controlled experiment with *Boophilus microplus* is described.

4. FOOD AND FOOD HABITS

Allen, M. D. & Selman, I. W. (1955). Egg-production in the mustard beetle, *Phaedon cochleariae* (F.) in relation to diets of mineral-deficient leaves. *Bull. Ent. Res,* **46,** 393-397.

Egg production reduced when diets deficient in nitrogen, phosphorus, potassium or iron were fed.

Buxton, P. A. (1954). British Diptera associated with fungi. 2. Diptera bred from Myxomycetes. *Proc. R. Ent. Soc. Lond.* (A) **29,** 163-171.

Certain Myxomycetes are the food organism for three species of Mycetophilid flies (*Mycetophila vittipes*, *Platurocypta testata* and *P. punctum*). Includes a list of other Diptera some of which appear to be generally saprophagous and others accidentals.

Davis, R. A. (1955). The coypu. *Discovery,* **16,** 237-239.

Particular mention is made of the East Anglian colonies of coypu (*Myocastor coypus*). The effects of the animal on growing crops are not significant, nor does it cause bank damage by burrowing. Food plants are listed; beds of reeds (*Phragmites communis*) have been cleared by the coypu, but in some places *Glyceria* has replaced *Phragmites* as it recovers more rapidly from grazing by coypu.

Eastham, L. E. S. & Eassa, Y. E. E. (1955). The feeding mechanism of the butterfly *Pieris brassicae* L. *Philos. Trans.* (B) **239,** 1-43.

A detailed anatomical account of the proboscis and associated structures. Critically examines and rejects previous theories as to the means of proboscis extension; offers a new explanation of the mechanism.

Gibb, J. (1954). Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis*, **96**, 513-543.

Repeated standard observations were made in a mixed broad-leaved wood. The frequency of feeding in different trees and shrubs, and at different stations was found to vary significantly from month to month. Though the several species of tit often eat the same foods, each species occupies a distinct feeding-niche.

Gibb, J. (1955). Feeding rates of great tits. *Brit. Birds*, **48**, 49-58.

Data obtained mechanically. By means of recorders which are fully described with diagrams the numbers and times of visits to the nest are automatically recorded.

Jones, A. W. (1955). Drone-fly visitors to the flowers on the City bombed sites. *Lond. Nat.* **34** (1954), 154-157.

Tables show for each of the five species (all in Eristalinae) present the total number of visits and the highest number on any one day, both for each month of 1954, and the total number of visits to flowers of seventeen plant species during the year. *Eristalis tenax* was the commonest syrphid and its status is discussed. Over 90% of the visits to flowers were to Compositae; none to umbelliferous plants was observed.

Leatherdale, D. (1955). Galls of *Rondaniola bursaria* (Dipt., Cecidomyiidae) eaten by slugs. *Ent. Mon. Mag.* **91**, 63.

Galls on *Glechoma hederacea* in which the larvae were almost mature were eaten by *Agriolimax reticulatus* and occasionally by *A. laevis* and *Arion intermedius*. No other parts of the plant, nor the fleshy galls made by the Cynipid, *Liposthenus glechomae*, were attacked.

Lockie, J. D. (1955). The breeding habits and food of short-eared owls after a vole plague. *Bird Study*, **2**, 53-69.

A discussion of predator-prey relationships during the decline of a short-tailed vole plague in Stirlingshire. During the spring of 1954, thirty to forty pairs of owls on 3500 acres were estimated to have taken 3 to 13% of the voles, which were then exposed owing to lack of cover, and this probably contributed to the decline of the voles. With the growth of cover, and the production of young by the voles, coupled with the disappearance of the owls after they had bred, only two pairs of birds remained, and the proportion of voles taken by these fell to between 2 and 6% of the population. Other predators included kestrels and foxes, the latter, together with crows, preying also on the owls at the nest.

Niblett, M. (1955). Some Diptera bred from fungi. *Ent. Rec.* **67**, 151-152.

Dates and localities for a Tipulid, a Mycetophilid and seven Muscids from Surrey of which all were reared from species of *Boletus* and *Lactarius* except for three for which the fungus attacked could not be determined.

Niblett, M. (1955). Some insect inhabitants of the knapweeds (*Centaurea* spp.). *Lond. Nat.* **34** (1954), 7-10.

Observations on the seasonal occurrence of Diptera and Hymenoptera bred from the flower-heads, leaves and stems of *C. scabiosa* and *C. nigra* over some twenty-five years.

Pearce, E. J. (1955). A note on the feeding-habits of Scydmaenidae and Prelaphidae (Col.). *Ent. Mon. Mag.* **91**, 29.

The Scydmaenid, *Cephennium thoracicum* is recorded preying on the Oribatid mite, *Galumna lanceolata*.

Simpson, J. (1955). The significance of the presence of pollen in the food of worker larvae of the Honey-bee. *Quart. J. Micr. Sci.* **96**, 117-120.

The larvae receive a variable quantity of pollen in their food in the summer and in winter sometimes none at all. This pollen probably provides the growing larvae with less than one-tenth of their total nitrogen requirement.

Southern, H. N. 1954. Tawny owls and their prey. *Ibis*, **96**, 384-410.

The diet of twenty pairs of *Strix aluco* living in woodland was followed for eight years by regular collection of pellets. A seasonal swing between small rodents in winter and spring and young moles, rabbits and rats in summer and autumn was regular, and is attributed to the difficulty of finding mice and voles when herbage is dense. Young tawny owls are dependent for about three months after fledging.

Williams, L. H. (1954). The feeding habits and food preferences of Acrididae and the factors which determine them. *Trans. R. Ent. Soc. Lond.* **105**, 423-454.

Observations and experiments with named British species suggest that the specific composition of the vegetation in the habitat is of little importance in limiting the distribution of the species.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Allen, A. A. (1955). *Rhizophagus aeneus* Richt. (Col., Rhizophagidae) new to Kent. *Ent. Mon. Mag.* **91**, 29.

R. aeneus is associated with timber in or near streams in northern and western England, but in west Kent was found in soil at the base of a small oak infested with *Cossus* away from water. The surrounding trees were oak and elm, with beech and exotic poplars.

Allen, A. A. (1955). *Agabus labiatus* Brahm (Col., Dytiscidae) in Herefordshire. *Ent. Mon. Mag.* **91**, 143.

A new county record.

Andrewes, C. H. (1955). *Dolichopus phaeopus* Walker (Dipt., Dolichopodidae) in Anglesey. *Ent. Mon. Mag.* **91**, 36.

Among *Limonium vulgare* in July 1953. This fly was hitherto known only from Hants. and Kent.

Andrewes, C. H. (1955). *Loxocera nigrifrons* Mcq. (Dipt., Psilidae) in Hertfordshire. *Ent. Mon. Mag.* **91**, 36.

Hitherto known only from the New Forest.

Arnold, G. A. & Arnold, M. A. 1954. Bird migration in the Tame Valley. *North. Nat.* (N.S.) **2**, 506-511.

Data on the numbers and direction of flight of migrating birds (passerines and waders), chiefly in autumn. After leaving the Trent Valley, most move south or south-west along the River Tame, though there is a definite westerly movement and a weak south-easterly one of small passerines; northerly or easterly movement is negligible during July-November. In spring, the direction of movement is north-west to south-west. Visible migration of small passerines is usually at 100 ft and most noticeable into slight or moderate head winds. Strong winds from any direction, continuous heavy rain, heavily overcast skies and fog are deterrents to migration, but bright periods with showers appear favourable.

Ashe, G. H. (1955). *Atheta Microdota alpina* Benick (Col., Staphylinidae) a species new to Britain in Devonshire. *Ent. Mon. Mag.* **91**, 28-29.

In an elm stump, in February 1954. Includes a translation of the original description of the adult.

Badcock, R. M. (1955). Widespread distribution in Britain of our allegedly rare caddis, *Hydropsyche fulvipes* Curtis (Trich., Hydropsychidae). *Ent. Mon. Mag.* **91**, 30-31.

This caddis, hitherto known only from Dorset and Somerset, was bred from larvae collected in Somerset, Staffs., Cheshire, west Yorks., north Lanes., Lanarkshire and Dumbartonshire and also occurs in Perthshire. Characters distinguishing the fifth-instar larvae from those of *H. angustipennis* and *H. pellucidula* are given.

Baird, R. H. (1955). A chiton, *Callochiton fulvus* (Wood), in the River Fal. *Nature, Lond.* **175,** 954.

Taken in Tolverne reach. Normal distribution Portugal, Spain and South America.

Barrow, R. L. (1955). *Omalus aeneus* F. (Hym., Chrysididae) in Worcestershire. *Ent. Mon. Mag.* **91,** 91.

A new county record.

Baynes, E. S. A. (1955). Report on migrant insects in Ireland for 1954. *Irish Nat. J* **11,** 286-287.

Lepidoptera, Orthoptera, Odonata.

Blackmore, M. (1955). The bats of Wales. *Nature in Wales,* **1** (2), 63-67.

Of twelve species of bats found in England, nine have been recorded for Wales. These are discussed individually with brief notes on their local distribution.

Blezard, E. (1955). Bats in Cumberland. *Northw. Nat.* (N.S.) **3,** 251-252.

Records of captures of five species in and near Carlisle, where *Myotis mystacinus* is the commonest species and *Nyctalis noctula* appears to be increasing.

Brown, R. G. B. (1955). The migration of the coot in relation to Britain. *Bird Study,* **2,** 135-142.

From analysis of ringing returns for west Europe. The general trend of movement is on a broad front passing north-east/south-west. Narrower movements follow the south Baltic, North Sea and north French coasts, and it is from these that coot enter Britain in winter. Data are insufficient as a guide to movements within Britain.

Campbell, J. L. (1955). *Lampra fimbriata* Schreb. (*Triphaena fimbria* L.) on the Isle of Canna. *Ent. Rec.* **67,** 240.

On 14 August 1955. The first record.

Claridge, M. F. (1955). *Ectobius lapponicus* L. (Orth., Blattidae) in Buckinghamshire and Northamptonshire. *Ent. Mon. Mag.* **91,** 81.

New county records.

Conisbee, L. R. (1955). A preliminary survey of the wild land mammals, of the Hastings district. *Hastings Nat.* **8,** 108-124.

A faunistic list, with various ecological details, such as habitat, food and cause of death.

Connell, J. H. (1955). *Elminius modestus* Darwin, a northward extension of range. *Nature, Lond.* **175,** 954.

Single specimen recorded from Farland Point, Isle of Cumbrae, Scotland. Settled 1954.

de Worms, C. G. M. (1955). The moths of London and its surroundings. *Lond. Nat* **34** (1954), 66-107.

Notes on localities, abundance, food plants and seasonal occurrence for species of the superfamily Agrotidae. (Cf. 1954, *Lond. Nat.* **33,** 101-146 (1955, *J. Anim. Ecol.* **24,** 215).)

Douglas, C. E. (1955). Ducks. *Reading Nat.* **7,** 3-7.

An assessment of the status in the Reading area of the sixteen ducks reported there, based on counts since 1947.

Duhig, M. & Humphries, C. (1955). *Amphilochus brunneus* Della Valle, an Amphipod new to Britain and Ireland and notes on other Amphipods not previously recorded in Irish coastal waters. *Proc. R. Irish Acad.* **57B,** 123-129.

Records the depth of dredging and, for bottom-living species, the type of bottom.

Ellison, N. F. (1954). Woodchat-shrike in Wirral, Cheshire. *Northw. Nat.* (N.S.) **2**, 462.

Includes notes, based on information from several observers, on feeding and other behaviour. The bird was seen to feed on bees and crane-flies, and was attacked and put to flight by a whitethroat feeding young.

Fernando, C. H. (1954). The possible dispersal of *Pisidium* by Corixidae (Hemiptera). *J. Conchol.* **24**, 17-19.

Small freshwater bivalves attach themselves to the claws of water-boatmen, suggesting a probable means of dispersal.

Ford, W. K. (1954). Lancashire and Cheshire Odonata (some further notes). *Northw. Nat.* (N.S.) **2**, 602-603.

Some additional records for eight species already noted. See 1953, *Northw. Nat.* N.S. **1**, 227-233 and abstract in 1955, *J. Anim. Ecol.* **24**, 238.)

Fryer, G. (1955). *Pomatocypris thienemanni* Klie, a little-known spring-inhabiting ostracod new to Britain. *Ann. Mag. Nat. Hist.* (12) **8**, 121-124.

Near Huddersfield. The habitat is described.

George, R. S. (1955). Some additional records of Arachnida from Gloucestershire, including four species of mites new to Great Britain. *Ent. Mon. Mag.* **91**, 121-124.

Numerous records, including eight spiders, two false-scorpions, four harvestmen and thirty-six mites new to the county.

George, R. S. (1955). Additional records of Hemiptera-Heteroptera from Monmouthshire. *Ent. Mon. Mag.* **91**, 143.

Contains twelve new county records.

Gibson, J. A. (1954). The breeding birds of Pladda. *Glasgow Bird Bull.* **3**, 55-56.

Notes on the twenty-two breeding species of this small island off Arran.

Gibson, J. A. (1954). The 1952 census of Gannets (*Sula bassana*) on Ailsa Craig *Glasgow Bird Bull.* **3**, 61-62.

7987 pairs were counted in 1952, an increase of 154 pairs on 1951.

Grensted, L. W. (1955). *Psychoda surcoufi* Tonn. and *P. humeralis* Mg. (Dipt., Psychodidae) in Gloucestershire. *Ent. Mon. Mag.* **91**, 98.

New county records.

Hale, W. G. (1955). Goosanders in spring. *Naturalist*, **1955**, 1-2.

Observations on *Mergus merganser* at a reservoir in the Lancashire Pennines, including notes on feeding habits.

Harwood, N. (1955). Bird movements on the north side of the Ribble Estuary, 1954. *Northw. Nat.* (N.S.) **3**, 68-75.

Observations on the numbers, which are shown for each month in a table, and movements of gulls and waders along a seven-mile stretch of coast between Lytham and St. Anne's during 1954. The results are discussed in detail and observations on behaviour are given.

Heslop-Harrison, J. W. (1955). The Lepidoptera of the Lesser Skye Isles. *Ent. Rec.* **67**, 141-147, 169-177.

Notes on the food plants and abundance of 310 species observed on the smaller islands round Skye, in vice-county 104. The flora and fauna of the islands to the east of Skye and Soay show affinities with the mainland and those of the islands further south with the Outer Isles.

Homes, R. C. (1955). Gull roosts of the London area. *Lond. Bird Rep.* **18** (1953), 37-39.

The numbers of gulls at the various roosts, based on estimates on a few dates during the winter of 1952-53 and 1953-54, were about 85 000-90 000 and about 90 000-100 000 respectively. Black-headed gulls were most abundant, and numbers of common, herring and great black-backed gulls were of the order of 10 000-15 000, 10 000 and upwards of 500 respectively.

Homes, R. C. (1955). Great crested grebes in the London area in autumn. *Lond. Bird Rep.* **18** (1953), 60-61.

The number passing through the London area appears to have changed little since 1930-38. By far the majority of passage birds congregate on the larger reservoirs and make little use of smaller waters and gravel pits.

Hurrell, H. G. (1955). The mammals of Devon. *Oryx*, **3**, 99-101.

Notes on bats, rodents, insectivores, deer and carnivores in various parts of Devon.

Jones, A. W. (1955). Notes on the butterflies of Wimbledon Common. *Lond. Nat.* **34** (1954), 108-114.

A systematic list of twenty-five species observed during 1947-54, with seasonal occurrence, abundance, habitats and flowers visited, and a list of plants showing flowering period, flower colour, and the species attracted to each.

Kevan, D. K. (1955). *Badister anomalus* (Perris) (Col., Carabidae) new to Britain. *Ent. Mon. Mag.* **91**, 6.

Collected in Dorset in July 1954.

Last, H. R. (1955). Two new British species of Staphylinidae (Col.). *Ent. Mon. Mag.* **91**, 106-107.

Atheta caucasia is recorded from east Inverness-shire in April 1946 and *A. boreella* in Leicester in July 1946.

McMillan, N. F. (1954). The Mollusca of Patrick's Wood, Bromborough, Cheshire. *J. Conchol.* **24**, 13-16.

Rich molluscan fauna in a calcareous woodland in otherwise non-calcareous district poor in land Mollusca.

McRitchie, J. A. (1955). The arrival of spring migrants, 1954. *Countryside*, **17**, 191-195.

Migrants in general were somewhat later in arrival than in 1953. The earliest cuckoo is shown as 21 March in Berkshire, but there is a record of a cuckoo having been heard and seen in Argyll on 26 February. Another interesting feature is the wintering of a redstart in Dorset.

Massee, A. M. (1955). The county distribution of the British Hemiptera-Heteroptera. Second edition. *Ent. Mon. Mag.* **91**, 7-27.

The presence or absence of 507 species in each of the counties of England and Wales and in Scotland and Ireland is shown, with the number of counties in which each occurs and the total number of species in each county in a chart that brings up to date and supersedes an earlier one (1945, *Ent. Mon. Mag.* **81**, 253-273) (cf. 1946, *J. Anim. Ecol.* **15**, 111) and a supplement (1946, *Ent. Mon. Mag.* **82**, 94-95).

Massee, A. M. (1955). *Physatocheila smreczynskii* China (Hem., Tingidae) new to Kent. *Ent. Mon. Mag.* **91**, 124.

Matheson, C. (1955). The carnivores of Wales. *Nature in Wales*, **1** (1), 22-24.

A brief account of the present status of each of the seven carnivores found in the principality.

Matheson, C. (1955). The rodents of Wales. *Nature in Wales*, **1** (3), 111-115.

A brief account of the present and past status of the fourteen species found in Wales.

Mathews, G. V. T. (1955). Animal migration. *Nature, Lond.* **176,** 772-773.

An account of papers read at the British Association symposium on migration.

Matthews, L. H. (1955). Marine mammals of west Wales. *Nature in Wales*, **1** (2), 49-53.

Notes on the Grey Seal and the cetaceans found round the west Wales coast.

Miles, P. M. (1955). *Parasitus setosus* Oudms. et Vgts. (Arachnida, Gamasidae) a mite new to Britain. *Ent. Mon. Mag.* **91,** 75.

On spent hops in Cardiganshire in September 1954.

Millidge, A. F. & Locket, G. H. (1955). New and rare British spiders. *Ann. Mag. Nat. Hist.* (12) **8,** 161-173.

Key to *Zora*. Many distributional records.

Murgatroyd, J. H. (1955). Some additions to the county records of spiders. *Ent. Mon. Mag.* **91,** 56.

Additions to the lists for Dorset, Beds., Notts., Somerset, Anglesey, Lancs. and Westmorland.

Nye, E. R. (1955). The flies of the London area. II. Culicidae sub-family Culicinae (mosquitoes). With a key to the species of *Culex*. *Lond. Nat.* **34** (1954), 114-126.

Localities and notes on the habitats and life-cycle of the twenty-four mosquitoes known in the London area, with a key to the five British species of *Culex*.

Philipson, G. N. (1955). Trichoptera in Northumberland. *Ent. Mon. Mag.* **91,** 3.

A list of some forty species believed to be new to the county, with dates and localities.

Pickard, B. C. (1955). The status of *Chorthippus mollis* (Charpentier) in Jersey, Channel Islands. (Saltatoria, Acrididae.) *Entomologist*, **88,** 137-138.

The author considers that this species does not occur in Jersey.

Ratcliffe, D. A. (1955). Cumberland dragonflies. *Northn. Nat.* (N.S.) **3,** 134-135.

Includes ecological data for five localities in which *Lestes sponsa* was found breeding in 1947 and 1950 and for one in which *Leucorrhinia dubia* was found breeding, for the second time in Cumberland, in 1950.

Rigden, R. G. (1955). The fishes, amphibians, reptiles and mammals of Woolwich and surrounding localities. *Lond. Nat.* **34** (1954), 48-53.

Localities and dates mostly 1954-55 for seven fish, six amphibians, three reptiles and twenty-four mammals.

Robson, R. W. (1954). On the great grey shrike in north Westmorland. *Northn. Nat.* (N.S.) **2,** 365-366.

This irregular winter visitor usually remains in one area only for a day or two, but in 1953 one was present at least from 27 November till 21 December and kept to a defined territory in which food larders were found.

Roe, K. M. (1955). Genus *Paraphyllopodopsyllus* Lang. (Copepoda Harp.): two new species—*P. hibernicus* and *P. hardingi*. *Proc. R. Irish Acad.* **57B,** 131-139.

Descriptions of two new species from the littoral zone of County Dublin.

Satchell, J. E. (1955). *Allolobophora limicola*—an earthworm new to Britain. *Ann. Mag. Nat. Hist.* (12) **8,** 224.

Description of habitat and comparison with foreign records.

Shearer, W. M. (1955). 'Homing instinct' in Sea Trout. *Nature, Lond.* **176,** 171-172.

Six tagged sea trout were recaptured the following year in the burns in which they had been marked.

Smith, K. G. V. (1955). *Syrphus arcuatus* Fln. (Dipt., Syrphidae) in Hampshire and Dorset. *Ent. Mon. Mag.* **91,** 119.

This syrphid was hitherto recorded only from Scotland.

Snow, D. W. (1953). Visible migration in the British Isles: a review. *Ibis,* **95,** 242-270.

The principal recorded observations on visible migration in the British Isles are brought together. The directions taken by a few species are discussed and shown on maps, and differences in behaviour are mentioned.

Southgate, B. J. (1955). Notes on the distribution of *Hallodapus montandoni* (Reut.) and other Hemiptera in Somerset. *Ent. Mon. Mag.* **91,** 75.

Includes four new county records.

Spencer, K. A. (1955). Notes on the British Agromyzidae (Dipt.). IV. A revision of the Hamm collection. *Ent. Mon. Mag.* **91,** 68-70.

Includes records of nine species new to Britain, some with food plants and localities.

Stratton, L. W. (1955). *Clausilia dubia* Draparnaud in the Malham area. *J. Conchol.* **24,** 41-46.

Detailed study of the habitats of a local land snail in a limestone area of West Riding, Yorkshire.

Stroyan, H. L. G. (1955). Recent additions to the British aphid fauna. Part II. *Trans. R. Ent. Soc. Lond.* **106,** 283-340.

Notes on seventy-two species with original descriptions of *Dactynotus riparius* and *Aspidaphum cuspidati*. Appendix A records corrections and additions to Part I (Stroyan, H. L. G., 1950, *Trans. R. Ent. Soc. Lond.* **101,** 89-124) and Appendix B refers to two recently recognized species: *Myzus certus* and *Sappaphis devecta*.

Taylor, C. E. & Gair, R. (1954). A preliminary annotated list of aphids of certain east midland counties. *Northw. Nat.* (N.S.) **2,** 512-525.

A list, with food plants, localities and dates, of species collected on plants in Derbyshire, Leicestershire, Nottinghamshire and Lincolnshire (Lindsey and Kesteven), and another of species taken only in traps.

Taylor, E. (1955). Seaweed flies (Diptera, Coelopidae) at Oxford. *Ent. Mon. Mag.* **91,** 97.

Coelopa frigida was recorded from Oxfordshire for the first time in November 1953, when swarms occurred at an infirmary, where they were attracted to chloroform and xylene, and a dry-cleaning establishment, where they congregated at a point where exhaust gases from the trichlorethylene cleaning apparatus impinged on a wall. Of twenty adults of both sexes dissected, some 80% of each sex were mature. The swarms were probably carried in by prevalent southerly and westerly winds.

Taylor, E. (1955). *Drosophila repleta* Wollaston (Dipt., Drosophilidae) at Oxford. *Ent. Mon. Mag.* **91,** 109.

A new county record.

Thomas, J. F. (1955). The Laugharne-Pendine burrows. *Nature in Wales*, **1** (2), 72-74.

Notes on the plants, birds, mammals and insects of these sand-dunes.

Thomson, A. L. (1953). The study of the visible migration of birds: an introductory review. *Ibis*, **95**, 165-180.

An introduction to a series of papers on visible migration in western Europe and the Mediterranean.

Whalley, P. E. S. (1954). List of birds seen in Anglesey and Caernarvonshire with notes on their distribution and status. *Northw. Nat.* (N.S.) **2**, 604-618.

A report of observations by the University College of North Wales Biological Society Bird Group over the past eight years.

Wheeler, A. S. (1955). A preliminary list of the Macro Lepidoptera of Bookham Common. *Lond. Nat.* **34** (1954), 28-36.

A list of 274 species, some taken at car lights, with indications of abundance and, in some cases, distribution and dates.

Williams, T. S. (1955). Notes on the bird life of the City of Chester. *Proc. Lpool Nat. Fld Cl.* **1954**, 30-32.

The first part of a paper on the birds of the city, and how they have adapted themselves to an urban environment.

Wood-Baker, C. S. (1955). Further records of European aphids (Hem.). *Ent. Mon. Mag.* **91**, 60-63.

Includes localities in Britain, dates and food plants for some twenty species.

Woodroffe, G. E. (1955). *Poeciloscytus palustris* Reut. and *Teratocoris antennatus* (Boh.) (Hem., Miridae) in Buckinghamshire and *Cyrtorhinus flaveolus* (Reut.) (Hem., Miridae) in Surrey. *Ent. Mon. Mag.* **91**, 36.

Additions to the county lists. The true habitat of *C. flaveolus* is stated to be deep in damp debris surrounding large tufts of *Deschampsia* and not, as was earlier thought, at the base of *Juncus* (cf. 1953, *Entomologist*, **86**, 34-40; 1953, *J. Anim. Ecol.* **22**, 387).

Woodroffe, G. E. (1955). A note on some Hemiptera-Heteroptera from Egham, Surrey. *Ent. Mon. Mag.* **91**, 54.

The dry-grass species, *Leptopterna ferrugata*, *Lopus decolor* and *Amblytylus affinis*, were dominant in a marshy habitat where the nymphs were swarming at the bases of *Juncus* and grasses even where growing in standing water. Records of other species present in this habitat, which comprised a bank separating two arable fields at different levels, are included.

Woollatt, L. H. (1955). The male of *Halidamia affinis* Fallén (Hym., Tenthredinidae) in Britain. *Ent. Mon. Mag.* **91**, 143.

This species was hitherto thought to be entirely parthenogenetic in Britain, but two males were taken in Devon 1951 and 1952.

6. STUDIES ON BEHAVIOUR

Airey, A. F. (1954). Diving of great crested grebes in the English Lake District. *Northw. Nat.* (N.S.) **2**, 504-505.

On Esthwaite Water and Blelham Tarn, these birds frequently dive and swim under water for considerably longer periods and distances than those recorded for the rest of England and Wales. The habit appears to be correlated with the extensive territory per pair. Dives of 70 yd by adults and 30 yd by birds about seven weeks old were observed.

Bagnall-Oakley, R. P. (1955). Display of snipe. *Brit. Birds,* **48,** 279-280.

The display (threat?) is performed when one bird approaches another too closely, or when other waders feed with snipe.

Balch, C. C. (1955). Sleep in ruminants. *Nature, Lond.* **175,** 940-941.

Kymograph records show respiration rate, reticulo-ruminal motility and whether the animal is standing, lying, resting or ruminating. It is concluded that if sleep occurs at all it is of a light and transient nature. This is related to the fact that the thorax must be kept upright for the efficient functioning of reticulo-rumen, and the time necessary for rumination.

Betts, M. M. (1955). The behaviour of a pair of great tits at the nest. *Brit. Birds,* **48,** 77-82.

Observations at a specially constructed nest-box. The share of the sexes in feeding the young, nest sanitation, the time spent by the female in brooding, and the times of awakening and roosting of the adults are noted.

Carrick, R. & Dunnet, G. M. (1954). The breeding of the fulmar *Fulmarus glacialis*. *Ibis,* **96,** 356-370.

A study during three seasons of marked birds. No marked individual changed its nest site, and no changes of mates occurred among marked pairs that nested in two consecutive years. A colony subject to avian but not wild mammalian predation showed a wide range of habitat and a strong tendency towards concentration.

Crowe, R. W. (1955). Parental care in the whitethroat. *Brit. Birds,* **48,** 254-260.

Behaviour after fledging is included.

Eccles, L. (1955). Whinchats choosing nest-site. *Brit. Birds,* **48,** 421-422.

The cock drove the hen from one site, but was in attendance when she brought material to another.

Goodwin, D. (1953). Observations on voice and behaviour of the red-legged partridge *Alectoris rufa*. *Ibis,* **95,** 581-614.

Observations on captive and wild birds. Call notes and their functions, display, nesting, parental care, feeding behaviour of chicks and fear responses are described.

Goodwin, D. (1955). Some observations on the reproductive behaviour of rooks. *Brit. Birds,* **48,** 97-105.

Nest building, displays, sexual behaviour, feeding of young and nesting and incubation by an unpaired female are described.

Griffiths, J. (1955). Jackdaw roost continuing throughout breeding season. *Brit. Birds,* **48,** 139.

Large numbers roosted regularly April to June in a roost used in winter.

Hinde, R. A. (1954). Factors governing the changes in strength of a partially inborn response, as shown by the mobbing behaviour of the chaffinch (*Fringilla coelebs*).
I. The nature of the response and an examination of its course. *Proc. Roy. Soc.* (B) **142,** 306-331.
II. The waning of the response. Ibid., **142,** 331-358.

Part I surveys the nature of the mobbing response made by wild-caught chaffinches, kept singly in cages, to models of owls, live owls and some other predators. Mobbing movements of other Fringillidae are briefly compared with those of chaffinches. Part II examines the process of decrement in the response to the same models and non-flying predators and the habituation of caged chaffinches to predators.

Hulme, D. C. (1955). Buildings as song-posts. *Brit. Birds,* **48,** 211-215.

Observations made for a year on a daily cycle journey through a built-up area with trees and gardens. Eight species sang from buildings, the gable end ridge tile being most favoured except by starlings which strongly preferred chimney stacks.

King, B. (1955). Pseudo-sleeping attitude of snipe. *Brit. Birds,* **48,** 232.

Two instances described, the bird squatting close with bill laid down the back.

Lord, J. (1955). Defence behaviour of a flock of coot. *Brit. Birds,* **48,** 176.

A scattered flock collected hurriedly into a compact circular body when a herring gull dived over them. The consequent splashing appeared to be incidental rather than deliberate.

Matthews, G. V. T. (1954). Some aspects of incubation in the Manx shearwater *Procellaria puffinus,* with particular reference to chilling resistance in the embryo. *Ibis,* **96,** 432-440.

Eggs are rarely subject to chilling, but hatched in the burrow after being chilled for up to seven days, and in the laboratory thirteen days. The survival value in this species is not apparent.

Mitchell, K. D. G. (1955). Aircraft observations of birds in flight. *Brit. Birds,* **48,** 59-70.

Observations made on scheduled passenger flights indicate that there is little flight by birds at heights of 500 ft or above in Britain. Twenty-one species of wild birds are represented in the records.

Radford, M. C. (1955). Nuthatch roosting times in relation to light as measured with a photometer. *Brit. Birds,* **48,** 71-74.

It is concluded that light does not affect the hour of roosting. (See also Radford, M.C., 1954, *Brit. Birds,* **47,** 166-168. Abstract in 1955, *J. Anim. Ecol.* **24,** 497.)

Rankin, W. T. C. (1954). Hibernation of hairy sand wasps, *Podalonia viatica* (L.), in numbers. *Northw. Nat.* (N.S.) **2,** 650-651.

Thirty-four adults were found on 21 October 1954, under loose bark in a small, decaying pine stump.

Raynsford, L. J. (1955). Goldcrest roosting in disused boring of woodpecker. *Brit. Birds,* **48,** 285-286.

The bird was flushed from the hole on four occasions. Hole-roosting is apparently unrecorded hitherto for goldcrest.

Ribbands, C. R. (1954). Communication between honeybees. 1: The response of crop-attached bees to the scent of their crop. *Proc. R. Ent. Soc. Lond.* (A) **29,** 141-144.

Results of the experiments outlined indicate that the addition of the scent to which the bees were trained approximately doubled the chance that they would go to their feeding place outside the visiting time to which they had been trained. The role of scent and dancing in recruitment to crops is discussed.

Ribbands, R. (1955). The scent language of honeybees. *Discovery,* **16,** 22-26.

Food sharing is the basis of communication in the honeybee colony since it is associated with the production of distinctive odours and so with the recognition of companions and the defence of the colony. It enables worker bees to be appraised of the presence of the queen so that in the event of any deficiency another is reared, enables new foragers to learn about suitable crops and helps to ensure an effective division of labour in the colony.

Robson, R. W. (1955). Tree sparrow's nest built into occupied buzzard's nest. *Brit. Birds,* **48,** 189.

Two instances are given.

Simmons, K. E. L. (1954). Further notes on house-sparrow behaviour. *Ibis*, **96**, 478-480. (See Simmons, K. E. L., 1952, *Brit. Birds*, **45**, 323-325.)

Observations on display, chasing, fighting for food and dust-bathing.

Simmons, K. E. L. (1955). The significance of voice in the behaviour of the little ringed and Kentish plovers. *Brit. Birds*, **48**, 106-114.

Has appendix 'The B.B.C. Little Ringed Plover recordings,' by E. Simms and E. R. Parrinder (pp. 114-115).

Snow, D. W. (1955). The abnormal breeding of birds in the winter 1953-54. *Brit. Birds*, **48**, 120-126.

Many reports of birds breeding, mostly in November and December, are related to the weather. Success was recorded for song thrush and blackbird.

Took, G. E. (1955). Nesting of herring gulls on roof-tops in Dover. *Brit. Birds*, **48**. 88-89.

A colony of 200 pairs is well established.

Wallace, D. I. M. (1955). Nightingale threatening cairn terrier. *Brit. Birds*, **48**, 422-423.

One of a pair of nightingales with fledged young drove the dog away by its display.

Warren, E. F. (1955). The fledging of a brood of ravens. *Brit. Birds*, **48**, 172-175.

The behaviour of the parents and young observed closely during and after fledging.

7. REPORTS OF ORGANIZATIONS

Birmingham and West Midland Bird Club (1955). The West Midland Bird Report, no. 21 for 1954. pp. 64.

In addition to the usual faunistic list of the birds seen in Warwickshire, Worcestershire and Staffordshire during the year, contains short papers on the birds of the Malvern district, swift migration in north Warwickshire in autumn 1954, the buzzard population of the three counties, and the birds of Cannock Reservoir.

Cambridge Bird Club (1955). Report for 1954. pp. 28.

Besides the usual faunistic list of birds seen in the county during the year, contains notes on migration, duck counts in the fenland, and wader counts at Cambridge sewage farm.

Cornwall Bird-watching and Preservation Society (1955.) Twenty-fourth Annual Report, 1954. pp. 58.

Besides the usual faunistic list of birds seen in the county during the year, contains short articles on the birds of the Camel estuary, the Scilly Isles and Tamar Lake near Bude.

Devon Bird-watching and Preservation Society (1955). Twenty-seventh Report, 1954. pp. 78.

Besides the usual faunistic list of birds seen in the county during the year, contains short papers or notes on black redstart migration, spotted flycatcher breeding biology, the heronry and duck censuses, and the Wembury and Spreacombe sanctuaries.

Fair Isle Bird Observatory (1955). Annual Report, 1954. pp. 24.

Summarizes the work done at the observatory during the year, mainly on migration, ectoparasites and the breeding of the arctic skua and fulmar.

Liverpool Naturalists' Field Club (1955). Proceedings and natural history notes for the area, 1954. pp. 32.

Includes notes on birds seen in the area during the year, on local non-marine Mollusca, on changes in the Dee marshes, 1951-54, and on local biting flies.

Lundy Field Society (1955). Eighth Annual Report, 1954. pp. 46.

Besides the usual faunistic lists of birds and mammals seen on the island during the year, includes short notes or articles on migration and ringing, the dispersal of shags, nesting sea-birds and ectoparasites.

Norfolk Naturalists' Trust (1955). The Norfolk Bird Report, 1954. pp. 46.

Besides the usual faunistic list of birds recorded in the county during the year, contains notes on the breeding birds of the Trust's six sanctuaries, on Scroby Sands off Yarmouth, and on the work of the Cley Bird Observatory.

Oundle School Natural History Society (1955). Annual Report, 1954. pp. 64.

Contains reports on vertebrates, Crustacea, spiders, butterflies, Ephemeroptera (including the ecology of the nymphs), freshwater gastropods, Platyhelminthes and Rotifera; also a note on the distribution of *Spirorbis spirillum* and *S. borealis* on the shore at Millport, Scotland.

des Forges, G. & Harber, D. D. (1955). The Sussex Bird Report, 1954. pp. 24.

Contains the usual faunistic list of birds seen in the county during the year.

Yorkshire Naturalists' Union (1955). Ninety-third Annual Report. *Naturalist*, **1955**, 11-31.

Includes faunistic notes in the usual zoological sectional reports for Vertebrates, Conchology and Entomology (Lepidoptera, Hemiptera, Odonata, Coleoptera, Orthoptera, Neuroptera, Hymenoptera, Diptera and Plant Galls).

Yorkshire Naturalists' Union (Vertebrate Section) Ornithological Division (1955). Report for 1954. *Naturalist*, **1955**, 67-93.

Includes the usual annual reports on the Spurn Bird Observatory and on the birds of Yorkshire during the year, arranged in the Wetmore order for the first time.

BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING AT ABERDEEN

16-21 JULY 1955

Members assembled during the morning of 16 July and after lunch a party went out to Hazlehead Woods on the outskirts of the city. Here a halt was first made to see *Cryptothallus mirabilis* and the party then walked through a beech wood. Where undisturbed much of the woodland floor was in the bare stage, but in places colonized by *Oxalis acetosella* or covered by *Vaccinium myrtillus* with *Oxalis*. The effects of the gale of January 1953 were observed with the consequent damage to the beech and changes in the ground flora, in which *Deschampsia flexuosa* and *Chamaenerion angustifolium* had replaced the other species. A small patch of pine wood was also seen with typical ground flora including *Ptilium crista-castrensis*. After passing through some of the public gardens of Hazlehead House tea was had before the party returned to the hostel. On the way back a halt was made to pay homage to the Rubislaw granite quarry.

Sunday 17 July was spent at the Sands of Forvie under the leadership of Mrs Landsberg. Starting in the southern part the sites of two Iron-Age dwellings were first examined and almost bare dunes inspected together with the soil profile. The party then proceeded generally northwards over successive dune ridges drifting at right angles to the coast. After passing over a large dune ridge of smooth sand and vigorous *Ammophila*, some time was spent in an area between two of the advancing dunes, where an interesting and fairly rich damp pasture vegetation was examined in some detail. Among the species found here were *Ophioglossum vulgatum, Climacium dendroides, Marchantia polymorpha, Juncus articulatus, Epilobium pedunculare, Carex maritima* and *Radiola linoides*.

Most of the party then worked towards the sea shore, where a patch of ' squeaking' sand was crossed and vigorous flowering *Kakile* seen. The party then moved inland again past the ruins of the medieval chapel of Forvie, and over a *Carex-Ammophila* grassland on thinner sand. Lunch was eaten in the shelter of a steep dune ridge on an *Empetrum* heath near a ternery. Nearby communities were dominated by *Cladonia sylvatica, Calluna vulgaris* and *Erica tetralix*, and other species were *Cetraria aculeata, Salix repens, Goodyera repens* and *Platanthera chlorantha*. After crossing an older eroding dune ridge an area of damp ground surrounding some shallow pools was reached, where abundant species were *Littorella uniflora Apium inundatum* and *Isolepis setacea*. Entomologists made collections in the pools and in Sand Loch. A walk over stable pasture led to the bus at Collieston and then tea at the Udny Arms, Newburgh, before the return south to Aberdeen.

During the day some members collected agarics and bryophytes and after tea a small party visited a nearby 'slack' where Miss E. M. Burnett pointed out *Haplomitrium hookeri* and other interesting species.

On Monday 18 July the excursion was up Deeside to Creag-an-Dail Bheag. The bus went north of the Dee and joined the main road at Kincardine O'Neill. Shortly afterwards some fine *Erica cinerea* was seen on Dinnet moor, and oak and pine forests at Ballater and Ballochbuie. In many places there were signs of logging in attempts to clear the damage done by the 1953 gale. At Inver Hotel a stop was made to have coffee and the party was joined by students from Southampton under the leadership of Dr Lambert. The bus was left in the Invercauld Estate (by kind permission of Captain Farquharson) and a track winding through open pine woods and on to the *Callunetum* slopes followed for about three miles to the head of the valley of the Glas Allt Bheag.

Lunch was eaten about half way up the hillsides on comfortable tussocks of *Empetrum* and *Calluna*. The lunch-time view was graced by the appearance on the skyline opposite of some sixty stags; a fine sight and one of the most rewarding of the meeting. After lunch plant-hunting began in earnest and species were rapidly ticked off on the list provided. Among the more interesting were *Astragalus alpinus, Dryas octopetala* and *Betula nana*. Many of these were found on the damp flushes of the gentle slopes on the far side of the summit or the drier flushes of the crags below. The exposed summit slopes showed good examples of erosion steps of dwarf *Calluna vulgaris, Empetrum hermaphroditum* and *Loiseleuria procumbens*. Several hares were seen and one ptarmigan flew by. Bryophytes collected included

several new to the vice-county, and interesting collections of Plecoptera and other insects were made in the Glas Allt Bheag. Although thick clouds concealed the summits of the nearby Cairngorms, no rain fell and summit temperature and wind conditions were nearly optimal. After rejoining the bus we were taken to Braemar for an excellent tea before returning to Aberdeen along the south Deeside road.

Tuesday 19 July began with a discussion in the Botany Department on *Calluneta* in north-east Scotland, and about thirty members and guests were present. The President was in the chair.

Dr C. H. Gimmingham opened the discussion with a review of two aspects of heather-dominated communities; their origins and the behaviour of the dominant under different conditions. *Calluneta* in the area were probably derived from former pine and oak woodland, drained, raised or valley bogs, steep and exposed hill and mountain slopes, and old non-calcareous dunes. Growth-form in *Calluna*, which has subsequent effects upon the community, is influenced by soil type, grazing and burning, and exposure.

Dr R. A. Robertson followed with an account of the geology and soils of the Glensaugh experimental farm. The farm straddles the Highland Boundary Fault, and includes soils on the pre-silurian quartz, mica schists and schistose-grits, and the Old Red Sandstones and conglomerates, though much of the lower slopes are covered by drift. There is an extensive area of hill peat dominated by *Calluna* and *Eriophorum vaginatum*, and podsols on the higher ground. Peaty gleys and brown forest soils occur elsewhere in the area. Correlations have been made between the vegetation and the soils.

Mr I. A. Nicholson described some of the *Calluneta* at Glensaugh in detail and paid particular attention to the height and growth-form of heather in four characteristic types. He showed that the abundance and status of associated species differed among the four types of communities and also that the proportions of the total cover contributed by representatives of a series of life-forms were markedly different in the four. Floristic, growth-form and life-form data were together adequate to describe the difference in structure and composition. The three papers were followed by a vigorous discussion which covered a wide range of topics connected with *Calluneta* and their utilization, such as podsols and pan formation, productivity under different management, loss of nitrogen on burning, genetic variation in *Calluna*, and quaternary forest history in north-eastern Scotland.

In the afternoon the meeting went by bus up picturesque Glen Dye to the Hill Farming Research Organization's experimental farm at Glensaugh to see some of the *Calluneta* discussed in the morning. The party, led by Mr Nicholson and Dr Robertson, left the bus at the summit of Cairn o'Mount and after being shown a typical soil profile under vigorous *Calluna*, traversed across the hill to see a series of communities in different stages of regeneration after fire, and the effect of burning heather of different ages. During descent to the farm experiments in dressing plots with lime and phosphates were pointed out, and while taking tea outside the farmhouse we were shown the effects on the vegetation of differing intensities of sheep grazing in enclosures on the hill opposite.

Wednesday 20 July was spent at St. Cyrus about thirty-five miles south of Aberdeen. The day was sunny and admirable for the full enjoyment of this interesting and attractive spot. The floral vigour of several gay species was at once apparent. Notable among these were *Campanula glomerata*, *Anchusa sempervirens* and *Silene nutans*. From the top of the cliffs the three main habitats—cliffs, dunes and salt-marsh—were clearly seen, while the seaward sweep of sand was dominated by the nets of the salmon fishery.

The meeting split up into small groups each of which concentrated on their particular interests. The rocky stacks were visited, and much time was spent on the cliffs and the talus slopes at their feet where, among several interesting species, were found: *Astragalus glycyphyllos*, *Echium vulgare*, *Trifolium scabrum*, *T. strictum*, *Vicia sylvatica*. On the steeper cliffs towards the south were the nests of fulmars and other sea birds. Between the cliffs and the back of the single dune ridge the flat area was covered with a pasture, until 1955 grazed by rabbits, and containing a rich collection of species including *Astragalus danicus*, *Dianthus deltoides*, *Geranium sanguineum*, *Origanum vulgare*, etc. At the southern end of the area is a small salt marsh on a sandy substratum. Here a large stand of *Scirpus maritimus* and rings of *Triglochin maritimum* were notable features, but detailed observation was prevented by a rising spring tide. After a tea in the village of St. Cyrus the party returned to Aberdeen. As on previous days, collections of mosses yielded species not previously seen in the area.

On the evening of Wednesday 20 July an informal discussion on myxomatosis was held at Hilton Hostel. This was opened by Dr Thompson who gave a brief but very clear account of the history and main features of the present outbreak in Britain. The outbreak started at Edenbridge in Kent in October 1953 and by the middle of 1955 few counties had not had

outbreaks. In England local transmission appeared to be due largely to the rabbit flea, and the rate of spread was about three miles per month. The kill in the field in England was 99% and there was little definite evidence yet of any attenuation of the virulence of the virus or any immunity being built up in the rabbit population. This outbreak of myxomatosis was likely to be the most important event in the ecological history of British wildlife since the rabbit had been introduced. There were already signs of the effect upon crops and natural vegetation, but the effect on the natural fauna was not yet clear, though observations on foxes, buzzards and hares were in progress.

Dr Morison followed with some observations on the parasites of the rabbit, particularly the flea. It seems that rabbits may support a large flea population but have few other arthropod parasites. Little is really known yet about the biology of the rabbit flea and its relation to the spread of myxomatosis; it does appear, however, that the virus may persist in the flea for some months. Dr Morison also mentioned some of the early and relatively unsuccessful attempts to introduce myxomatosis into some of the Scottish and Irish islands. Some discussion followed these two papers on aspects of the animal ecology of myxomatosis. Among the points raised was that of the effect upon some of the rarer animals and birds such as the kite in Wales and wild cat in Scotland.

Dr Hope-Simpson followed and discussed the possible effects of the reduction in rabbits on some types of natural and semi-natural vegetation. He thought that the succession, grassland→scrub→woodland, would be encouraged and accelerated. The show of flowers would be increased but the encouragement of rank species might lead to the loss of some less vigorous interesting species. The importance of the intelligent use by farmers of land previously dominated by rabbits was stressed.

Many members took part in the subsequent discussion and differences of opinion were shown over several points. The symposium and discussion as a whole evoked considerable interest and it was agreed that the subject should be aired again in a year or two's time.

The last day of the meeting, Thursday 21 July, was spent visiting laboratories in Aberdeen. In the morning a large party went to the Macaulay Institute for Soil Research where members were greeted by Dr Macarthur and then toured the various sections of the Institute. Current lines of research were demonstrated and briefly explained, and great interest was shown in the work on pedology, X-ray analysis, thermal analysis of clay minerals, spectrographic analysis, soil fertility, organic matter, soil microbiology and plant physiology, and in the progress of the Scottish Soil Survey. Some members also inspected the grounds and gardens.

A small party of animal ecologists visited the Department of Zoology in Marischal College. Here we were welcomed by Professor Wynne-Edwards and other members of the staff and were shown over the department, museum and other parts of the College including the tower.

In the afternoon about half the members went to the Marine Laboratory of the Scottish Home Department. Here after a welcome from Dr Lucas we were able to admire the new building and were shown round several excellent exhibits illustrating current research into chemistry, plankton, herrings, haddock and other fishes. We were then shown two films on Scottish fishing, one an excellent underwater film of seine-netting.

Thus ended a most successful summer meeting. The Society is very grateful to Professor Matthews for the hospitality of his Department, to the several local ecologists who helped to guide the excursions, to the staffs of the institutes we visited on the last day, to the Warden and Staff of Hilton Hostel who made us so comfortable, and finally to Dr Gimmingham for making all the arrangements for such an excellent and smoothly organized meeting.

E. D. LE CREN

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDED DECEMBER 31ST, 1955

1954	Income	£ s. d.	£ s. d.
	Subscriptions received, including arrears and *less* payments in advance:		
	Members taking *Journal of Ecology* only	586 4 3	
	Members taking *Journal of Animal Ecology* only	322 13 11	
	Members taking both Journals	387 8 1	
	Associates	5 4 6	
1237			1301 10 9
	Interest Received:		
	Investments	162 0 0	
	Deposit Account	12 18 7	
	Post Office Savings Bank Account	72 13 8	
215			247 12 3
	Journal of Ecology, Index to Volumes 1-20:		
	Sales	21 2 0	
	Less Costs	8 14 6	
10			12 7 6
3	*Watson's Census Catalogue of British Lichens*—Sales		— — —
—	*Net Deficit for the year transferred to Balance Sheet*		62 2 7
1465			£1623 13 1
	Journal of Ecology:		
1623	Sales: Current Volume 43	1711 0 10	
446	Back Volumes and Parts	521 13 5	
145	Reprints of Papers	215 18 3	
15	Advertising space	15 2 6	
			2463 15 0
20	Contribution to Cost of Plates		40 0 0
			2503 15 0
734	Loss on Journal transferred to Revenue Account		689 18 6
2983			£3193 13 6
	Journal of Animal Ecology:		
1081	Sales: Current Volume 24		1162 19 6
644	Back Volumes and Parts		647 15 10
100	Reprints of Papers		103 9 4
			1914 4 8
37	Loss on Journal transferred to Revenue Account		493 14 3

1954	Expenditure	£ s. d.	£ s. d.
	Working Expenses:		
	Expenses of Meetings	61 6 2	
	Clerical Assistance	8 7 6	
	Audit Fee	15 15 0	
	Postages, etc.	14 6 4	
	Printing and Stationery	16 18 4	
	Travelling	12 16 3	
	Addressograph, Stencils, etc.	17 10	
	Telephone and Telegrams	5 14 3	
	Bank Charges	1 4	
118			136 3 0
	Grants:		
	Freshwater Biological Association	10 0 0	
	British Co-ordinating Committee for Nature Conservation	4 4 0	
12			14 4 0
	Journal of Ecology:		
734	Costs *less* Sales		689 18 6
	Journal of Animal Ecology:		
37	Costs *less* Sales		493 14 3
	Biological Flora of British Isles:		
	Costs	403 14 6	
	Less Sales	114 1 2	
233			289 13 4
331	Surplus for the year		— — —
1465			£1623 13 1
	Journal of Ecology:		
2599	Costs: Printing, Paper, Blocks and Binding		2746 6 3
268	Publisher's Commission		292 3 0
109	Carriage, etc.		138 4 6
5	Insurance of Stock		7 12 2
1	Editor's Expenses		3 0 7
1	Miscellaneous Expenses		6 7 0
2983			£3193 13 6
	Journal of Animal Ecology:		
	Costs: Printing, Paper, Blocks and Binding:		
	Volume 17 (extra copies)	330 0 0	
	Current Volume 24	1749 5 7	
1535			2079 5 7
214	Publisher's Commission		225 8 1
54	Carriage, etc.		62 9 1
20	Fee for Checking References		20 0 0
14	Insurance of Stock		14 1 8
6	Editor's Expenses		5 4 6
19	Miscellaneous Expenses		1 10 0

BALANCE SHEET AS AT DECEMBER 31ST, 1955

Assets

1954		£ s. d.	£ s. d.
	Cash at Westminster Bank:		
	Current Account	363 6 4	
	Deposit Account	100 0 0	
2216			463 6 4
3825	Post Office Savings Bank Account ...		2897 5 0
4	Sundry payment in advance		4 2 6
	Publishers Account due:		
	Cambridge University Press—		
	Journal of Ecology	34 3 8	
	Journal of Animal Ecology	1020 13 2	
	Biological Flora of British Isles ...	39 0 7	
	Journal of Ecology—Index to Vols. 1-20	4 19 0	
—			1098 16 5
	Sundry Accounts due:		
	Journal of Ecology	15 0	
	Journal of Animal Ecology	24 7 8	
—			25 2 8
	Commissioners of Inland Revenue:		
—	Income Tax recoverable		25 10 0
	Investments at Cost:		
	£700 of 3% Post Office Savings Bonds, 1960/70	700 0 0	
	£300 of 3% Post Office Savings Bonds, 1965/75	300 0 0	
	£1000 of 3% Redemption Stock, 1986/96	1005 18 6	
	£1200 of 3½% War Stock	1230 4 1	
	£1500 of 4% Federation of Rhodesia and Nyasaland Stock, 1972/74 ...	1519 3 0	
3236			4755 5 7
9281			£9269 8 6

A further asset, not valued, is the stock of Journals, Index Volumes and Biological Flora Reprints held for the Society by the Publishers.

VICTOR S. SUMMERHAYES
C. E. HUBBARD
Hon. Treasurers

Liabilities

1954		£ s. d.	£ s. d.
	Members' Subscriptions paid in advance		
48	for 1956/61		46 5 8
1	Library Fund		1 5 0
	Printing Account owing:		
	Cambridge University Press—		
744	*Journal of Animal Ecology*		798 12 4
	Sundry Accounts owing:		
	Postage	5 13 2	
	Printing and Stationery	9 6	
9			6 2 8
	General Revenue Account:		
	Surplus in hand at December 31st, 1954	8479 5 5	
	Less Net Deficit for the year ended December 31st, 1955	62 2 7	
8479			8417 2 10
9281			£9269 8 6

We have examined the Balance Sheet and Income and Expenditure Accounts of the British Ecological Society as at December 31st, 1955, set forth above. We have obtained all the information and explanations we have required, and have verified the investments and Balance at Bank. In our opinion the above Balance Sheet is properly drawn up as to exhibit a true and correct view of the state of the Society's affairs, according to the best of our information and the explanations given us, and as shown by the books of the Society.

RYLAND CLIFT & CO.
Incorporated Accountants

10 ECCLESTON PLACE
WESTMINSTER, S.W.1
February 24th, 1956

NOTICE TO CONTRIBUTORS

Contributors are asked to study these notes with care in order to save themselves and the editor unnecessary work in the revision of manuscripts.

1. All correspondence should be addressed : **The Editor, Journal of Animal Ecology, The Ferry House, Ambleside, Westmorland.**

2. TEXT. MSS should be typed double-spaced on one side of the paper, leaving top and left-hand margins at least an inch wide. Latin names of genera and species, **but nothing else,** should be underlined. Dates should be in the form '1 Jan. 1956, 25 June' etc., not 'Jan. 1st', or with the month indicated by a figure. Text-figures are to be referred to as 'Fig. 1', etc. In the use of symbols, signs and abbreviations *British Standard 1991: Part I: 1954* should be followed, including the omission of all unnecessary full stops.

The *Journal's* conventions regarding cross-headings should be followed, but they should not be used too freely, **nor should headings be underlined.** Only long papers need include a table of contents. The Royal Society's *General notes on the preparation of scientific papers* should be followed on points not mentioned here.

3. LATIN NAMES. Excepting those of British vertebrates, all Latin specific names should be followed by the authority when the name is first mentioned in the text or tables. Names must be verified either from a standard list such as Kloet and Hincks's *Check-List of British Insects* or by submitting the final MS to the experts who have supplied the identifications.

4. REFERENCES should be listed in alphabetical order at the end of the paper in the form :

Vevers, H. G. & Fisher, J. (1938). The 1938 census of gannets (*Salu bassana*) on Ailsa Craig. *J. Anim. Ecol.* **7,** 303-4.

Titles of journals should be abbreviated according to the *World List of Scientific Periodicals,* except that the English usage of capitals for adjectives should be followed. Any reference not personally seen should be marked with an asterisk. **Nothing** except Latin names of genera and species should be underlined, nor should titles of papers or books be put in inverted commas.

5. TABLES should be set out on separate sheets and numbered in arabic numerals. So far as possible sufficient description should be included in the headings to make tables self-explanatory. The layout of tables should be kept as simple as possible ; they are not printed 'boxed'.

6. TEXT-FIGURES. Drawings should be in jet-black indian ink, preferably on Bristol board. Shading must consist of lines or dots, not of half-tone washes. If the addition of mechanical stippling or hatching is required the area should be indicated by hatching lightly in blue pencil. Drawings should be arranged or grouped so that after suitable reduction a figure about 5 in. wide results. Graphs should be drawn on paper ruled in blue or faint grey ; axes and graduation marks must be drawn in indian ink. All lettering, numerals and arrows should be shown lightly in pencil for insertion in uniform style by the blockmaker. The author's name and the number of the figure should be written on the back of each. Legends for figures should be collected together at the end of the MS.

7. PLATES. Photographs will only be used to illustrate important points which cannot conveniently be shown in any other way. Unmounted, glossy, half-plate prints showing good detail and moderate, but not excessive, contrast, are required. They should be numbered separately from text-figures, and each print should bear on its back the number and the author's name.

8. PROOFS. Page-proofs only will be sent. They should be returned with the least possible delay, and the minimum of essential correction should be made. Authors are requested to pay particular attention to the checking of numerical matter, mathematical formulae, tables and lists of names.

9. REPRINTS. Authors are supplied with 50 reprints gratis. Additional copies may be purchased if ordered when the proofs are returned. Contributors from abroad should order when sending their MSS. Reprints are sent out about a month after publication.